The Effect of Potassium Upon the Uptake and Distribution of Magnesium in Plants.

by

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submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy

UNIVERSITY OF TASMANIA

HOBART

December, 1968.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and to the best of my knowledge contains no copy or paraphrase of material previously published or written by any other person except where due reference is made in the text of the thesis.

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November, 1968.

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ACKNOWLEDGMENTS.

Many people contributed to the work of this thesis.

In particular, I would like to acknowledge the contributions made by the following:

The Rural Credits Fund of the Reserve Bank of Australia who supported the student for three years of the project, and who made a special grant for the purchase of an atomic adsorption spectrophotometer, essential to the research programme.

Professor G. C. Wade, Dean of the Faculty of Agriculture, whose efforts attracted the support to the programme.

Dr. J. A. Beattie, Senior Lecturer in Soil Science, supervisor of the project, who over the three years, showed more understanding than I perhaps deserved.

Dr. K. C. Marshall, Reader in Agricultural Microbiology and Dr. R. C. Menary, Lecturer in Horticulture, who were constant sources of useful advice and partners in beneficial discussion.

Messrs. R. Wheatley, C. Mathews and G. Ley of the University Workshops, whose helpful co-operation produced much of the apparatus used in this study.

Finally, the whole project would not have been possible without the encouragement and co-operation of my wife, Marie, and my family, who cheerfully gave up economic security and an established home and interests, so that I could undertake the work reported.

SUMMARY.

Applications of potassium fertilisers may reduce the amount of magnesium in plants, at times to a degree which produces symptoms of magnesium deficiency. As well as its effects on the availability of soil magnesium, potassium affects the amount of magnesium in the plant in two ways: by competition at the site of uptake, thus resulting in a lower total plant magnesium, or by reducing transport of magnesium between plant organs. There is disagreement on the relative importance of these factors.

The kinetics of short term uptake of potassium and magnesium by detached barley roots were studied by methods based on the Michaelis-Menten theory of enzyme-substrate relationships. These experiments showed competitive inhibition of magnesium by potassium but not of potassium by magnesium. This may be explained by proposing that there are many sites of potassium uptake and that some of them are free of magnesium competition. Competitive inhibition of a divalent ion by a monovalent ion has not been observed previously, earlier reports being confined to competition between ions of like valency. An apparent stimulation of potassium uptake by magnesium was found to be due to the influence of a common anion (chloride).

Short term uptake experiments with whole barley plants showed that, under some circumstances, potassium interfered with translocation of magnesium from root to top. This finding was supported by results of split root experiments.

Split root and plant injection experiments showed that translocation of magnesium from root to tops was reduced

by potassium, that elevated leaf potassium stimulated the efflux of leaf magnesium, and that K/Mg ratios were better correlated with symptom expression than the levels of each element alone.

The effects of potassium and magnesium on the growth of barley plants and the distribution of various ions within the plant during development, were studied in sand culture. In this experiment, potassium reduced the uptake of magnesium but the results disagreed with the findings of the short term experiments. For example, added magnesium reduced the amount of potassium taken up even though the plant magnesium level was unchanged. In addition, potassium did not interfere with the translocation of magnesium in this experiment. The effects of magnesium on development and on the Mg, K, Ca, Na, and P content of the main stem and first tiller were examined. High potassium decreased the sodium content of all plant parts. High magnesium decreased the uptake of phosphorus in this work, although it has been shown by other workers that additions of magnesium increased phosphorus content, particularly of the seeds. The chemical composition of the inflorescence was changed little even though that of the vegetative parts varied widely.

1. INTRODUCTION.

Magnesium deficiency has been reported in numerous horticultural and field crops grown on many soil types throughout the world. It has been recognised, over a long period, that potassium fertilizers reduce the amount of magnesium in plants, often to the stage where magnesium deficiency symptoms develop. In addition, hypomagnesaemia of both sheep and cattle has been associated with the ingestion of herbage low in magnesium. As agriculture intensifies and higher rates of potassium fertilizer are used, there is an increasing danger that potassium induced deficiency of plants and animals will become more widespread.

The amount of magnesium present in plant tops can be affected by reducing the available magnesium in the soil, by reducing uptake through competition between magnesium and other ions during absorption, or by reducing transport of magnesium from roots to tops. In most soils potassium adversely affects the amount of magnesium available to the plant. There is however, disagreement on the relative importance of the two plant factors. Many workers maintain that uptake of magnesium is adversely affected by the presence of potassium ion. Others maintain that, in some plants at least, the total amount of plant magnesium is unaffected by the presence of potassium in the medium, but that it accumulates in the roots until finally net magnesium influx is reduced to zero.

There is some confusion about the mobility of leaf magnesium. Recently several authors have failed to find evidence of leaf magnesium mobility in specific instances. The fact that deficiency symptoms invariably occur first on the older leaves has been taken, however, to indicate that magnesium is mobile, the order of symptom development being a consequence of magnesium redistribution from older to younger leaves and growing points. In addition, diurnal variation in leaf magnesium can only be explained in terms of mobile leaf magnesium.

The object of the present study was to establish whether potassium nutrition reduced total plant magnesium and to determine the importance of competition between these ions at uptake and within the plant. The kinetics of magnesium and potassium uptake by detached barley roots was studied using a modification of the technique described by Epstein and Hagen (1952). Split root and plant injection techniques were used to examine competition between the elements within the plant, and to examine K/Mg ratios in relation to symptom expression. The effect of potassium on the distribution of magnesium in the developing plant was investigated using whole plants which were grown at different potassium levels and harvested at different stages of development.

11. LITERATURE REVIEW.

MAGNESIUM DEFICIENCY AND ITS DISTRIBUTION.

Magnesium deficiency was first recognised by Garner et al. (1922, 1923) who cured "sand drown" of tobacco by the application of magnesium. Wallace (1925) first recognised the disease in apples in sand culture. The deficiency was recognised in potatoes (Carolus 1933) and citrus (Parbery 1935, Fudge 1938, 1939) soon after.

Field occurrence of magnesium deficiency in apples, was first reported in England (Wallace 1939, Hoblyn 1941). After this the condition was found in many parts of the world, Canada (Hill and Johnston 1939), New Zealand (Kidson et al. 1940) and U.S.A. (Boynton 1945).

Magnesium deficiency is common to a great range of horticultural and field crops (Wallace 1951; Childers 1966). However, there is a considerable variation between genera and between species. Wallace (1951) says that members of the genus Brassica all appear very susceptible. Varieties of a species can also vary in susceptibility as Foy and Barber (1958) found for corn. Eisenmenger and Kucinski (1947) suggest that magnesium deficiency is more common in the lower orders of seed plants.

Deficiency of this nutrient produces a wide range of symptoms in plants, particularly on the foliage. Potatoes and some clovers become chlorotic and tinted with red anthosyanins. Some Brassica species develop brilliant yellow, orange, red and purple tints. Other plants show varying degrees and patterns of chlorosis, followed by necrosis. Many of these symptoms are illustrated in colour by Hambridge (1941) and Wallace (1951).

Never-the-less there is a basic developmental pattern for the deficiency which is common to most plants

(Wallace 1951). This pattern may be outlined as follows: -

(1) Symptoms are most outstanding on the foliage, always developing initially on the older leaves and proceeding towards the younger ones. This is indicative of nutrient mobility within the plant. When deficiency levels are encountered by the plant, magnesium appears to be mobilised from the mature leaves to the young growing parts (Wallace 1951).

(ii) Chlorosis is common, as would be expected from the fact that magnesium is an essential constituent of chlorophyll (Willstatter 1906).

(iii) In addition, bright anthocyanin colours develop (Wallace 1951).

(iv) Severely affected leaves may absciss, with or without previous withering. Defoliation may be extremely severe as is the case in apple trees. In extreme cases the tree may be left bearing no leaves except at shoot tips and is unable to ripen the current crop (Wallace 1951). The lack of photosynthetic area would also reduce the carbohydrate reserves in the tree and thus affect the future crop (Priestly 1962). In addition, premature loss of leaf could cause a reduction in the amount of abscisic acid (abscisin II or dormin) in the tree (Carns 1966) and consequently upset dormancy in the following winter.

Magnesium deficiency symptoms are often more common towards the end of the growing season, when, under low magnesium conditions, magnesium from the older leaves has been redistributed to the growing points and developing fruit (Kidson 1946).

Reports of magnesium deficiency in the field in Tasmania have been confined to apples (Ward 1957) and one isolated

report in cauliflower (Anon. 1968). In addition magnesium deficiency of tomatoes, grown under glasshouse conditions, with high levels of potassium, has been observed. This deficiency, both in field and glass-house tomatoes, has been reported from several countries (Cromwell and Hunter 1942; Hunter 1946; McNaught and Gdanitz 1952 a & b; Weber 1955), and has been shown to be related to potassium status (Cromwell and Hunter 1942; Walsh and Clarke 1945 b; Winsor *et al.* 1965). A similar relationship between potassium and magnesium deficiency in apples has been widely reported (Hill and Johnston 1939; Kidson *et al.* 1940; Boynton *et al.* 1943; Southwick 1943; Boynton and Burrell 1944; Southwick and Smith 1945; Cain 1948, 1953 a & b; Cain and Boynton 1948).

Magnesium deficiency in pasture species under field conditions has been reported by several workers (Stephens and Donald 1958; Dorofaeff and McNaught 1962; de Wit *et al.* 1963; McNaught and Dorofaeff 1965). Animals grazing pasture low in magnesium are liable to contract hypomagnesaemia. Kemp and t'Hart (1957) and Todd (1961) set the critical level at 0.2% magnesium in the plant dry matter. In contrast symptoms of plant magnesium deficiency do not occur until lower levels are reached, for example, 0.06% for grass (de Wit *et al.* 1963) and 0.12% for white and 0.14% for red clover (McNaught and Dorofaeff 1965). In this case, hypomagnesaemia may occur in animals although pasture plants show no symptoms.

Potassium top dressing of pastures can cause hypomagnesaemia by reducing the amount of magnesium available to animals (Wolton 1963). This is aggravated by the fact that high levels of ingested potassium reduce the blood magnesium of the grazing animal (Kunkel *et al.* 1953; Fontenot *et al.* 1960) and by the apparent ability of animals to selectively graze plants high in potassium (Paton 1956; Field 1967).

Increased use of potassium could therefore bring loss of production in several types of agricultural production and it is certain that the use of this fertilizer will increase. Coleman (1963) suggests that world consumption of potassium fertilizers will increase 57% in the decade 1960-1970. Much of this will be used on increased acreage brought into production but a considerable quantity will be used to increase the rate of application on established areas. The Tasmanian situation is similar. The increase in potassium fertilizer applied to pasture since 1953 is shown in Figure 1. The ratio of potassium used to acres of sown pasture was 43 in 1957-58 and had dropped to 24 in 1965-6. This suggests that the application to pastures cannot be completely accounted for by increased acreage. Paton (1950, 1956) discovered extensive areas of potassium deficiency in old established agricultural areas. Correction of this deficiency would account for some of the increased usage.

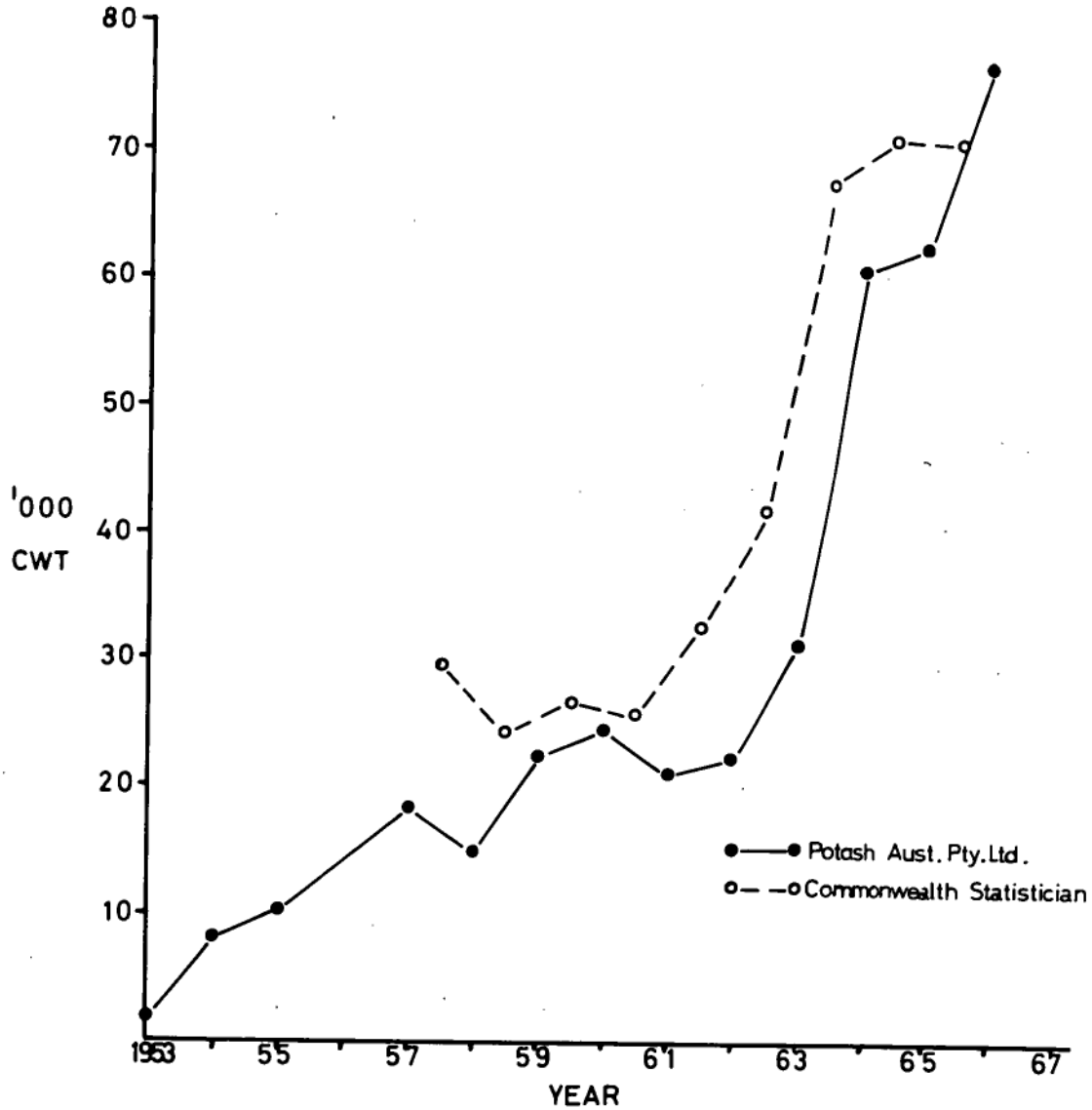
FUNCTIONS OF POTASSIUM AND MAGNESIUM.

The functions of potassium in plants have been reviewed by Pirson (1955) and only an outline and some mention of more recent work will be given here.

The full role of potassium in plants is still unknown. It is essential to all plants and cannot be replaced completely by sodium, lithium or rubidium, elements which are chemically similar (Pirson 1955). Potassium is found in plants mainly as soluble inorganic salts and to some extent as salts of organic acids. Metabolically active and meristematic regions, buds, root tips and young leaves, contain high levels of potassium often at the expense of older, mature tissues, the element being very mobile and readily distributed within the plant during development (Löhr 1953; Williams 1955).

FIGURE 1.

Amount of potassium fertilizer applied annually to Tasmanian pastures.


80
70
60
50
40
30
20
10
'000
CWT
1953
55
57
59
61
63
65
67
YEAR
Potash Aust. Pty. Ltd.
Commonwealth Statistician

Potassium deficiency is associated with many changes in plants. Leaf damage is a conspicuous consequence of low potassium levels. It has been recorded in many plants, Brassica (Hewitt 1953, 1954), apples (Wallace 1928 a and b), cocoa, hops, beet, broad beans (Wallace 1951), potatoes (Kenten and Mann 1951; Kenten 1955), citrus (Camp et al. 1941), subterranean clover (Millikan 1953) and many others.

Changes in growth also occur. In many plants the internodes are shortened and apical dominance is reduced (Richards and Templeman 1936; Richards and Shih 1940; Camp et al. 1941 and Millikan 1953). In addition leaf growth is reduced (Njoku 1957). Cambial activity can be reduced or lost (Janssen and Bartholemew 1929; Penston 1931; Nightingale et al. 1930).

Chlorosis is commonly associated with potassium deficiency and in some plants, for example, citrus (Camp et al. 1941), beans, lucerne, clovers, tomatoes, mustard, Brassica, grasses and some apple varieties (Hewitt 1963) depressed chlorophyll production has been noted. Kidson (1942) related the potassium and magnesium distribution in the leaf to the chlorotic pattern displayed.

Richards and Shih (1940) found that the water content of plants increased in consequence of decreased potassium levels. In support of this finding, Goodall et al. (1957) found that potassium was implicated in the variation in the water content of lettuce which was brought about by changes in phosphorus status.

Over a long period, evidence has been advanced that the carbo-hydrate metabolism of plants is disturbed by low potassium levels (Gregory and Richards 1929; Gregory and Baptiste 1936; Richards 1932, 1938; Briggs 1932; Nightingale et al. 1930; Janssen and Bartholemew 1929; Hartt 1934 a and b; Richards and Templeman 1936; Gregory and Sen 1937; Cooil and Slattery 1948. Sugiyama et al. (1968) found that activity of pyruvate kinase was enhanced early

in the onset of potassium deficiency. Supply of potassium restored normal enzyme activity, and along with it normal carbohydrate and chlorophyll levels, in about three days. Reversal of early potassium deficiency symptoms has been observed previously. (Wall 1940; Evans and Sorger 1966). It has not yet been established that the level of pyruvate kinase activity is directly related to the elevated carbohydrate levels commonly found in potassium deficient plants (Sugiyama et al 1968). Eaton (1952) related carbohydrate accumulation in plants to the associated impaired protein synthesis.

Impairment of protein synthesis has been described in this connection over a long period (Gregory and Richards 1929; Hartt 1934 a and b; Cooil and Slattery 1948; Eaton 1952). A specific catalytic role for potassium, in the synthesis of certain peptide bonds, has been described (Webster 1953 a and b; 1956; Webster and Varner 1954).

Potassium can also activate such enzymes as fructokinase, pyruvic acid kinase and trans acetylase, and many others (Evans and Sorger 1966). In such reactions, potassium is the most effective ion but other monovalent ions (Rb^+, NH_4^+ , and Na^+ in that order) also activate the mechanism (Colowick and Kaplan 1955; Miller and Evans 1957; McCollum et al. 1958; Griffin and Brown 1964). In a high proportion of the enzyme activations in which potassium is concerned, magnesium is also required. This may be one of the reasons why particular K/Mg ratios seem required for optimum plant health.

The early work on magnesium functions has been reviewed by Jacob (1955) and more recently by Gauch and Krauss(1959). The most obvious function of magnesium is associated with its role in the chlorophyll molecule (Willstatter 1906). This accounts for 10% of the leaf magnesium. The reason for this unique requirement of magnesium has not been satisfactorily explained.

Evidence indicates that magnesium deficiency inhibits cell division (Webb 1953) of bacteria, possibly through effects on amino-acid metabolism (Jungner 1951). Fleisher (1935) found that in Chlorella, cell division was inhibited by magnesium deficiency but cell growth continued.

Several workers have found a correlation between phosphorus and magnesium in plant tissues (Miller 1938; Mulder 1953; Zimmerman 1947). It has been suggested on this basis that magnesium is a carrier for phosphorus (Truog et al. 1947). The relationship may however be fortuitous. It is more likely due at least in part, to the fact that magnesium activates numerous enzymatic reactions involving phosphate, accounting for the concentration of both ions in rapidly developing tissues (Bear et al. 1951). However Stenlid (1959) maintains that magnesium alone of all divalent ions, stimulates uptake and transport of phosphorus by plants.

The correlation between active tissues, which are high in phosphate and magnesium content may also reflect the role of magnesium in stabilising the ATP molecule. The ATP molecule, as it exists in the cell, has four negative charges which are concentrated about its polyphosphate side chain. This is very unstable and usually little free ATP exists in the cell; stable soluble complexes with magnesium are normally found (Lehninger 1965). X-ray and spectroscopic analyses of the ATP molecule suggest that its magnesium complex does not exist in a fully extended form but in a curled up configuration so that the terminal phosphate groups are close to the 6-amino group of the adenine ring, the group important in actions of ATP where the terminal phosphate is transferred enzymatically. (Lehninger 1965).

Many functions of magnesium can be related to enzyme activity. Gauch and Krauss (1959) exhaustively reviewed

this subject and tabulated many reactions in which magnesium takes part as an activator of the enzyme involved. Phosphorylation by chloroplasts, catalase synthesis, glycolysis and related carbohydrate transformations, the Kreb's cycle, the alternative pentose cycle, lipid metabolism, nitrogen metabolism, reactions associated with the "phosphate pool" and photosynthesis have all been shown to involve magnesium activated enzymes.

It seems that magnesium plays a predominant role in enzyme activity associated, in particular, with carbohydrate metabolism. According to Nason and McElory (1963) magnesium mainly participates intimately in the reactions involving group transfer, namely those in which phosphate participates, by serving as an intermediate carrier.

Marinos (1963) discovered that low magnesium affects the function and adherance of plant mitochondria, causing the appearance of granules which are apparently associated with disintegration of mitochondrial cristae.

Nutrients can be detrimental to plants when present in excess as well as when deficient. Toxic effects of potassium have been reported in the literature. One of the earliest reports by Miyake (1913) suggests that potassium and magnesium are toxic to plants when applied separately but that the effect disappears when they are used together, or with calcium.

Again, this early work suggests that the K/Mg ratio may be important. The reduction of magnesium uptake by potassium, the subject of this study, may thus be considered as toxic effect of potassium. High potassium has also induced symptoms of iron chlorosis (Walsh and Clarke 1942) which may be associated with the induction of manganese toxicity by the elevated level of potassium (Martin and Bingham 1954; Vlamis and Williams 1962).

High levels of magnesium have also exhibited toxic effects. Some of these are associated with growth inhibition associated with increases in osmotic pressure (Wadleigh and Gauch 1944). Other effects have been observed such as disturbance of the K/Mg ratio (Trelease and Trelease 1931). Gauch (1940) found that elevated magnesium could reduce calcium to deficiency levels.

According to Hayward and Wadleigh (1949) high plant potassium disperses cellular colloids and thus disorganises the protoplasm. In contrast high magnesium acts as a coagulant. They point out that one of the main actions of magnesium is to regulate cell permeability.

Despite the number of specific functions of plant magnesium, Cain (1959) was able to point out that the function of 90% of the total plant magnesium was unknown. Similar vagueness surrounds much of the function of plant potassium. Recent work suggests that much of the plant content of these elements may be important in maintaining a specific K/Mg ratio.

Work on a variety of crops has shown that symptom expression is more closely related to K/Mg ratios than to the absolute level of either cation (Wallace 1925, 1947; Parbery 1935; Wallace *et al*. 1946; Nicholas 1948; Cain 1948; Prouwer 1951; Smith *et al*. 1954; Ferrari and Sluijsmans 1955; Forshey 1963.)

It is known that some specific enzyme reactions, as yet studied only in microorganisms and yeast, require both Mg^{++} and K^{+} for activation (Priess and Handler 1957, 1958; Ismande 1961; Snoke 1955). These reactions may also be important in higher plants.

Ribosomes, which were first isolated from higher plants in 1956 (T'so et al. 1956), are responsible for the synthesis of protein (McQuillen 1962; Bonner J. 1965). T'so and Vinograd (1961) showed that removal of Mg^{++} from the medium caused ribosomes to dissociate into their constituent particles. Recent work with micoorganisms, however, has strongly suggested that a correct K/Mg ratio, rather than magnesium alone, is responsible for ribosome stability and function (Tempest, Dicks and Hunter 1966).

This finding may give meaning to the presence of large quantities of "useless" Mg^{++} and K^{+} in plants and may provide a basis for explanation of the importance of the K/Mg ratios in optimum growth and yield of plants.

ION UPTAKE.

This subject has been extensively reviewed in the past (Laties 1959; Steward and Sutcliffe 1959; Sutcliffe 1962; Brouwer 1965).

The time course of ion uptake is characterised by a brief period of rapid uptake followed by a more prolonged period of slower absorption (Steward and Sutcliffe 1959; Stiles and Skedling 1940). These two periods can be contrasted in the following way;

The prolonged steady absorption is

a) suppressed by several respiration inhibitors and must therefore be dependent on respiration,

b) usually an obligate aerobic process with a high temperature coefficient,

c) usually concerned with the absorption of both members of an ion pair.

The rapid initial phase, on the other hand,

i) is a non-metabolic process (Broyer and Overstreet 1940; Broyer 1961), and even takes place in dead tissue (Broyer and Overstreet 1940; Steward and Harrison 1939;

Vervelde 1953),

ii) may occur anaerobically and has a temperature coefficient typical of physical processes (Sutcliffe 1954),

iii) is predominantly concerned with cation adsorption (Briggs 1957).

It appears that the initial stage of uptake is concerned with several processes of a physical nature. The first of these is entry into the apparent free space (A.F.S.). This space is the summation of the Donnan free space (D.F.S.) and the water free space (W.F.S.) The W.F.S. is actually an extension of the external environment, and solutes can enter it by diffusion. Briggs and Robertson (1957) consider W.F.S. to consist of wet cell walls and much of the cytoplasm, and many workers agree with this (Epstein 1956; Hylmö 1955; Laties et al. 1964; Lundegårdh 1955). Demonstration of the plasmalemma as a high resistance barrier for cations suggests that this view is not tenable (Lundegårdh 1958; Laties 1959; MacDonald and Laties 1963; MacRobbie and Dainty 1958; Spanswick and Williams 1964). It is likely therefore that W.F.S. is confined to regions outside the plasmalemma particularly as estimations of its volume by Ingelsten and Hylmö (1961) suggest that it occupies about 11% of wheat root tissue.

Specification of D.F.S. in anatomical terms is even more vague than that of the W.F.S. Some authors confine it to the cell wall (Brouwer 1954; Dainty and Hope 1959; Jansen et al. 1960; Winter 1961), others include cytoplasm (Briggs 1957; Leggett et al. 1962; Lundegårdh 1958). It has been estimated to make up 2-3% of root tissue (Briggs et al. 1958). There is no apparently physical demarkation between D.F.S. and W.F.S., indeed Briggs (1957)

and Briggs and Robertson (1957) ascribe part of the cytoplasm to both. Briggs et al. (1958) say the extent of the D.F.S. is governed by the distance over which electromotive forces are active, i.e. about 10 Å. Both cations and anions enter W.F.S. but D.F.S. contains mainly cations (Briggs 1957).

In the D.F.S. predominantly negative fixed charges, almost exclusively in the cell wall (Laties 1959), have hydrogen ions or other monovalent or divalent cations attached to them. Adsorption appears to be electrostatic (Overstreet 1957) and its extent depends on the type of ions under exchange; there is an apparent preference for divalent over monovalent cations (Brouwer 1965). Some anion exchange with the much fewer positively charged sites may occur (Epstein 1955; Jacobson and Overstreet 1947). Adsorption also appears to depend on the relative concentration of ions present and is relatively more important at low external concentrations than at high concentrations (Briggs 1957; Epstein 1955; Kylin and Hylmo 1957). Adsorption exchange has been shown to be a universal function of plant roots (Briggs et al. 1958; Hopkins 1956; Jacobson et al. 1957; Middleton and Russell 1958; Overstreet et al. 1952; Sutcliffe 1954).

In addition to adsorption exchange, Laties (1959) suggests that it is possible that non-specific, almost irreversible adsorption, of a type similar to that of charcoal, can take place in root tissue. This would be of importance only at very low concentration, if at all (Jacobson and Overstreet 1947; Overstreet and Jacobson 1946).

The hypothysis of a "carrier" which exchanges H^+ for other ions in the external solution, and having transferred the ions across the membrane, releases them to the interior of the cell, has been a useful basis for much experimental

work (Epstein and Hagen 1952; Epstein 1956). A similar transport system has been envisaged for anions (Jacobson et al. 1950; Sutcliffe 1962).

Adsorption exchange was thought by some workers to be the first stage of such ion uptake (Gonzalez and Jenny 1958; Higinbotham and Hanson 1955; Jacobson et al. 1950; Lundegårdh 1950; Russell and Ayland 1955; Sutcliffe 1954). The suggestion has even been made that adsorption sites are identical with the proposed carrier sites (Wohl and James 1942; Epstein and Hagen 1952). It is now considered that adsorption sites have little or nothing to do with absorption, although agreement about this is far from universal. (Laties 1959).

It has been established that species of high cation exchange capacity (C.E.C.) can attract and bond divalent cations with relatively more energy than those with a low C. E. C. (Mattson et al. 1949; Elgabaly and Wiklander 1949; Elgabaly and Abdel Ghani 1958; Asher and Ozanne 1961). By raising the C.E.C. of barley roots, White et al. (1965) established this variation within a species. It has been suggested (Asher and Ozanne 1961) that root C.E.C. may exert some influence on ion uptake by raising the concentration of cations in the D.F.S. above that of the surrounding solution and by influencing the proportion of ions of different valency in the D.F.S. as a consequence of the Donnan valence effect. It is suggested that these effects would be most noticeable when plants were growing in a medium of low ionic activity (Asher and Ozanne 1961).

A less obvious exchange, between ions and the carrier, which has been inferred from kinetic analysis of uptake data, has been suggested as an integral part of transport into the cell (Epstein 1956). Concentration of carrier sites

has been estimated from ion uptake behaviour and appears to differ markedly from that of adsorption sites (Hagen et al. 1957; Laties 1959).

Many other considerations suggest that carrier and adsorption exchange sites are separate. Epstein and Leggett (1954) found that when uptake was measured using a radioactive tracer, ions accummulated by adsorption exchange could be removed by equilibration with a non-radioactive solution of the same ion. Residual radio-activity gave a measure of absorption by the tissue and this was a linear function of time from the beginning of the uptake period. Since adsorption and absorption can be distinguished in this way, Laties (1959) suggests that it would be possible to establish apparent dissociation constants for the carrier-ion and exchange site-ion reactions.

High concentrations of fixed negative charges in the D.F.S. have been measured by Briggs (1957) and Briggs et al. (1958). As a consequence of this high concentration, anions fail to enter the D.F.S. to any extent at the concentrations usually used in uptake studies. Thus anion accummulation cannot be concerned with D.F.S. (Laties 1959) suggested that this must apply to cations as well - Epstein (1955) and Epstein and Leggett (1954) have shown that anions accumulate readily from the W.F.S. and that cations of the D.F.S. are unable to be absorbed. As cations and anions of a univalent salt are absorbed in equal quantities during steady state absorption (Steward and Harrison 1939), it would be expected that evidence of considerable anion adsorption would be recorded if adsorption is the first step in ion accumulation.

Work on the kinetics of adsorption and absorption such as carried out by Epstein and Hagen (1952), Hofstee (1952), Hagen and Hopkins (1955), Hagen et al. (1957), and Briggs (1957), indicates that the two processes are separate, for example competition between ions for carrier sites is very specific (Epstein 1953; and Epstein and Hagen 1952; Epstein and Leggett 1954). However, this work has received some

criticism.

Bange and van Gemerden (1963) suggest that the method of analysis used by these authors is not reliable depending as it does on the belief that removal of exchange adsorption ions by washing in distilled water does not affect the concentration of the ion-carrier complex. Briggs et al. (1961) also claim that the evidence for the existence of carriers is inadequate or open to other interpretations, for example, in terms of an anion pump (Briggs 1963). They call for more work with tissues in which the adsorption of single salts is well understood, particularly by experiments short enough to avoid toxic or metabolic effects on some ions.

ION TRANSPORT SYSTEMS.

According to Overstreet (1957) it is not necessary to postulate membranes and a series of carriers for ions, the carrier-ion complex passing through membranes which are impermeable to ions alone. His suggestion is that there is one complex "carrier" represented by the protoplast and that structures could be built up within a lattice in a manner similar to a crystal lattice. He and his co-workers (Overstreet et al. 1952) had found K^+ was more firmly bound to the cell when absorbed with Ca^{++} which suggested to him that they were possibly bound to a single structure. Overstreet (1957) considered it reasonable to assume that cations and anions were absorbed in proportions which increased the structural stability within the "carrier". This also allowed for the experimental observation that K^+ is more rapidly absorbed from KCl solutions than from K_2SO_4 solutions of equivalent concentrations. In other words, Overstreet sees the carrier, not as a discreet chemical structure, but as living protoplasm in which the ions are not free but held at various sites as an integral part of a very complicated but labile structure.

This suggestion now probably has some basis in physical reality with the demonstration of an endoplasmic

reticulum in most cells. This structure is continuous with the nuclear membrane, has ribosomes attached to it, fills a great part of the cytoplasm and impinges intimately on all other cellular structures (Thompson 1965). However, it was probably the fact that many workers had identified the plasmälemma by menas of electron microscopy (Briggs et al. 1961) which detracted from Overstreet's hypothesis and centred all discussion and experimentation firmly on the cell membrane.

The plasmälemma, outer membrane to the cytoplasm, has been observed in many electron microscope preparations but is not invariably demonstrable. When present it is about 100 Å thick (Briggs et al. 1961). It is now well accepted that such a membrane surrounds all cytoplasm and contains the "living" portion of the cell. Acceptance of this membrane as the primary membrane concerned with the regulation of ion uptake does not deny that other membrane (e.g. the tonoplast and mitochondrial membranes) may exhibit active transport and thus help decide the ultimate fate of ions which enter the cell.

The exchange membrane must be of low permeability to free ions (Collander 1959; Arisz 1964), capable of achieving accumulation of ions greatly in excess of their concentrations in the external solution (Steward and Sutcliffe 1959) and must exhibit a high degree of selectivity between ions even to the extent of discriminating successfully between chemically very similar ions (Epstein 1962).

Ion accumulation is curtailed, when metabolism is stopped or greatly reduced, as by low oxygen tensions (Hoagland 1944),

metabolic poisons (Ordin and Jacobson 1955) or low temperatures (Epstein et al. 1962; McDonald and Laties 1963). This obvious link between metabolism as a source of energy and ion absorption, has led to a prolonged search amongst the various facets of plant metabolism, in an attempt to identify ion carriers.

Any such search must inevitably centre on the mitochondria, in which the cytochrome system is located and oxidative phosphorylation takes place. Using isolated mitochondria, Robertson et al. (1955 a and b) and Honda and Robertson (1956), have demonstrated the ability of these organelles to accumulate ions. This has led them to suggest that these bodies act as the primary sites of accumulation and transport in the cytoplasm (Robertson 1960). Mitochondria are thought to move from the plasmalemma to the tonoplast where they break down and release ions to the vacuole. This requires the replacement of mitochondria after each transfer and therefore seems unlikely. However, mitochondria are probably an integral part of the system of ion transport by virtue of their central role in metabolism, even though their precise transport function is unknown.

The cytochrome system is located in the mitochondria (Bonner W. D. 1965; Lehninger 1964). The most comprehensive carrier hypothesis yet proposed involves a cytochrome acting as a carrier of ions, in addition to being an intermediate acceptor of electrons in respiration (Lundegardh 1955). This theory was first advanced by Lundegardh in 1939. Cations are thought to be absorbed passively under the influence of the electrical gradient produced by absorption of anions. This electrical gradient was said to be brought about by the movement outwards of electrons and hydrogen ions in amounts equivalent to the anions absorbed (Lundegardh 1954). The theory was based on the contention by Lundegardh

and Burstom (1933) that salt respiration, in contrast to endogenous respiration, is exactly correlated with ion absorption. Epstein (1954) showed stimulation of respiration by cation exchange resins, from which anions were not absorbed, so the anion, upon which Lundegardh's hypothesis is based, is not necessary.

There have been many other criticisms of the theory. If a single carrier is involved, anion competition should be demonstrable. This has been shown for bromine and chlorine but not for other anions (Helder 1952). Robertson et al. (1951) criticised the hypothesis because dinitrophenol inhibited salt uptake and yet respiration was stimulated. The stimulation is now known to be due to the uncoupling of the electron transport reaction from the phosphorylation of ADP to ATP. Under these circumstances, the energy of the reaction is not stored as ATP for use in functions such as uptake but is dissipated in increased respiration, (Lehninger 1965).

Sutcliffe and Hackett (1957) and Sutcliffe (1962) have succeeded experimentally in exceeding the maximum of four anions transferred for each molecule of oxygen which is dictated by the cytochrome hypothesis. It has been shown that anions and cations can be absorbed (Russell 1954; Lowenhaupt 1956; Laties 1959) by capacity built up by prior respiration, possibly in the form of ATP which usually performs such functions. This is in line with the much earlier suggestions of this possibility (Asprey 1937; Ketchum 1939). This is not covered by Lundegardh's hypothesis.

In addition it is difficult to see, if absorption of cations is passive along a gradient of electric potential, how the high selectivity that plants exhibit for cations can be explained. It seems unlikely that a system confined to the mitochondria of a cell could effectively act as a

carrier for ion uptake. It is more reasonable to suggest that the connection between respiration and ion uptake is due to the formation of ATP which is capable of diffusing from the mitochondria and being used in the region of the plasmalemma (Hendricks 1966).

Current opinion suggests that the energy for ion transport is provided in the mitochondria through the production of ATP by the electron transport activities carried out therein (Bonner W.D. 1965).

The effects of phosphorylation inhibitors, such as dinitrophenol, on salt absorption (Robertson et al. 1951) support this conclusion. However, the precise way in which the energy is utilised in active transport has yet to be determined. Hypotheses involving nucleic acid (Steward and Miller 1954) and lecethin (Bennet-Clark 1956) have been advanced.

A more recent theory is associated with the discovery of adenosine triphosphatase (ATPase) in animal cell membranes (Skou 1957; 1964; Dunham and Glynn 1961). A quantitative correlation has been found between the enzyme and ion transport in several tissues (Bonting and Caravaggio 1963), and the enzyme has been isolated from all animal tissues in which ion transport is sensitive to the glycoside ouabain or G-strophanthin (Bonting et al. 1962). The enzyme is stimulated by K^+ and Na^+ together (Skou 1957; Bonting et al 1961). ATPases with similar properties have been described in several micro-organisms (Schultz and Salmon 1962: Kleber and Aurich 1967).

Lehninger (1965) has described a model of the possible action of membrane bound ATPases and their function in ion transport. This is based on ATPase being held in a specific orientation in the membrane and thus, because ATP can only combine with the enzyme in a specific way, the direction of approach of ATP to the membrane is controlled.

The OH^- radicle approaches from the opposite side of the membrane, and after hydrolysis of the terminal phosphate, ADP and phosphate move towards the centre of the cell away from the ATPase. Thus a vectoral reaction is set up which results in excretion of H^+ across the membrane. ADP diffuses back to the mitochondria and ATP is reconstituted. This model can be modified to account for the behaviour of other cations.

Skou (1957) has shown that hydrolysis of ATP to ADP can be associated with the directional transport of K^+ and Na^+ across cell membranes in a manner very similar to that described for H^+ in the model. Cell membrane ATPase activity has been found to be greatly stimulated by K^+ and Na^+ (Skou 1957) but only if K^+ concentration is high outside and Na^+ concentration is high inside the cell. During hydrolysis of ATP, K^+ moves into and Na^+ out of the cell. This ATPase pump has been found in many animal cell membranes. The molecular details of K^+ and Na^+ movement by the ATPase are not known but it is apparently based on the action of a membrane fixed enzyme which can accept Na^+ from the inside and K^+ from the outside and release them at the opposite sides.

In addition to the K^+ and Na^+ activated ATPases mentioned earlier, Hafkenscheid and Bonting (1968) have described an ATPase from Escherichia coli which is activated by Mg^{++} as well. There is a basis for suggesting therefore that a model could be designed to include ATPase mediated uptake of Mg^{++} in plants.

Steenbjerg and Jakobsen (1963) considering the interaction between potassium and magnesium at uptake in plants, suggest that the mode of operation might be similar to the fructokinase -mediated production of fructose phosphate and ADP in the liver (Hers 1952). This reaction

has a specific K/Mg ratio requirement for optimum activity and Hers suggests that the enzyme has two reactive centres which combine with metals or their complexes. An enzyme with Mg-ATP attached at one site and K^+ at the other is a ctive, and all other possible combinations are inactive. Perhaps membrane bound ATPases can be similarly activated, need for Mg^{++} as well as K^+ and Na^+ having been established for several isolated ATPases.

Because of the obvious importance of ATPases in animal tissues and their potential value in explaining plant behaviour, a search has commenced for similar enzymes associated with plant cells, particularly in plant roots.

Brown et al (1965) isolated a membrane bound ATPase from the cotyledons of peanut which differed in some respects from the enzymes isolated from animal tissues. Gruener and Neumann (1966) found a soluble, Mg^{++} dependent ATPase in bean roots, which was markedly stimulated by several monovalent cations. However, it differed from animal ATPase in several respects and particularly in being insensitive to ouabain. Mengel (1963) found that rubidium absorption by barley roots was not sensitive to ouabain. The discovery of ouabain-sensitive ATPase in membranes of barley roots (Chattopadhyay and Brown 1966; Dodds and Ellis 1966) suggests that the effect of ouabain on ion uptake by barley roots should be more closely examined.

Further evidence of the association of ATPases with ion uptake of plants is provided by the work of McClurkin and McClurkin (1967). They demonstrated cytochemically a K^+ and a Na^+ activated ATPase associated with the roots and mycorrhizae of Loblolly pines. The sodium activated

enzyme occurred in the root meristems. The K^+ activated ATPase, on the other hand, was associated with the mycorrhiza. Pines absorb K^+ efficiently only when infected by mycorrhiza (Harley and Wilson 1959; MacDougall and Dufrenoy 1944; Routien and Dawson 1943). It appears therefore that the cation activators are specific and cannot be substituted by other cations. The authors suggest that such specific activation may be the basis for the plant's ability to distinguish between such ions as K^+ and Na^+ .

Pitman and Saddler (1967) have recently produced data for ion uptake by barley roots, which they interpret in terms of a reciprocal K^+ and Na^+ pump. This interpretation, if confirmed, would establish in plants a system very similar to that established for animal tissues.

INTERACTION BETWEEN IONS AND COMPETITION FOR CARRIERS.

Epstein and Hagen (1952) proposed absorption of ions by plant root cells is by means of carriers with which free ions combine in order to traverse barriers in the cell which are otherwise impermeable to them. The complex (carrier plus ion) crosses the barrier, and then breaks up, releasing the ion to the interior of the cell. They suggest that this system is analogous to the mechanism of catalysis mediated by enzymes. In both cases, the substance acted on (the ion or the enzyme) combines with an agent (the carrier or the substrate) to form an intermediate labile complex which is subsequently broken down. Interfering substances, may change the kinetics of the system by:

(a) combining with the agent at the same reactive centres which bind the substance being interfered with (competitive inhibition),

(b) combining with the agent or the complex at a site different to the one which binds the substance being interfered with (non-competitive inhibition),

(c) combining with the complex (uncompetitive inhibition). Considering the combination of enzyme and substrate as a reversible reaction, Michaelis and Menten (1913; in Fruton and Simmonds 1959) following expression for Km, the Michaelis constant:

$$K_m = S\left[\frac{V}{v} - 1\right] \quad \text{or} \quad v = \frac{V[S]}{K_m + [S]}$$

where V = maximum velocity

v = measured velocity

$[S]$ = concentration of substrate

The reciprocal of this expression is:

$$\frac{1}{v} = \frac{K_m + [S]}{V[S]} = \frac{K_m}{V}\left[\frac{1}{S} + \frac{1}{V}\right]$$

This is called the Lineweaver-Burk equation (Lineweaver and Burk 1934). Its value rests on the fact that if $1/v$ and $1/[S]$ are plotted, a straight line is obtained which is more convenient for determination of K_m and V.

Where an inhibiting substance, which combines with the enzyme at the same site, is introduced, the velocity of the reaction will depend on both the concentration of the substance and of the inhibitor. Then as pointed out by Epstein and Hagen (1952) the equation becomes:

$$\frac{1}{v} = \frac{1}{V}\left[K_m + \frac{K_m[I]}{K_i}\right]\frac{1}{[S]} + \frac{1}{V}$$

where $[I]$ is the concentration of inhibitor,

and K_i is the Michaelis constant for the inhibitor-enzyme complex.

Thus, if $1/[S]$ is plotted against $1/v$, there will be an increase by a factor of $1 + [I]/K_i$ in the slope of the line without a change in the intercept. This change in the graph is therefore typical of competitive inhibition.

In the case where the inhibitor combines with the enzyme, independently of the substrate and therefore at a point different to the one to which the substrate attaches itself, the velocity equation becomes:

$$\frac{1}{v} = \left[1 + \frac{[I]}{K_i}\right]\left[\frac{1}{V} + \frac{K_m}{V} \cdot \frac{1}{[S]}\right]$$

In this case, where $1/v$ is plotted against $1/[S]$, both the slope and the intercept are increased by a factor of $1 + [I]/K_i$. Thus it is easy to distinguish non-competitive and competitive inhibition.

Uncompetitive inhibition is where the inhibitor combines only with the substrate-enzyme complex and not with the enzyme at all.
Here the velocity equation is:

$$\frac{1}{v} = \left[1 + \frac{[I]}{K_i}\right] V + \frac{K_m}{V} \cdot \frac{1}{[S]}$$

When $1/v$ is plotted against $1/[S]$, the slope of the line is unchanged but the intercept is increased by a factor of $1 + [I]/K_i$.

If this type of thinking is applied to the carrier hypotheses of ion uptake, the substrate is equated with the ion whose uptake is being studied, the inhibitor with the interfering ion; and the enzyme with the carrier mechanism. Epstein and Hagen (1952) take pains to point out that it should not be assumed from this theory that the carrier mechanism is enzymatic. They emphasise only that the behaviour is analogous and that the use of the technique is profitable.

The work of Epstein and his co-workers has been criticised because there is no indication of the nature or location of the carrier. Steward and Sutcliffe (1959) maintain that such mathematical interpretation, applied to a system as heterogeneous as a plant root, has little meaning unless the specific mechanism is located. Epstein (1965) has defended the basis of his theory by drawing a parallel with early biochemists who were able to deduce many of the properties of enzymes and their mode of operation, before their chemical nature was elucidated.

Experiments based on the kinetic model developed by Epstein and his co-workers have produced a body of data which is useful in understanding the behaviour of ions and which will serve as a basis for future research. In addition, significant progress has been made towards the identification of the carrier, and indeed, despite the caution originally expressed by Epstein and Hagen (1952) a major component of the carrier system may be enzymatic.

One body of experimental results suggests that in terms of carriers, K^+ and Mg^{++} are absorbed by different carrier sites (Collander 1941; Scott 1943; Epstein and Leggett 1954; Moore *et al*. 1961. Potassium and sodium interact with one another and this is usually explained by assuming competition for a single site (Sutcliffe 1956, 1957; Jacobson *et al*. 1957; Fried and Noggle 1958; Bange 1959). Epstein and Hagen (1952) consider that there are two separate carrier sites for rubidium and sodium and, by inference, for potassium and sodium. Scott and Haward (1953, 1954) reach similar conclusions.

This contradiction possibly comes about because of the existence of two sites for the uptake of potassium (Kahn and Hanson 1957; Bange 1959). One of these sites transports potassium alone and is not influenced by sodium. The other is able to transport both sodium and potassium and both these ions compete for it when supplied simultaneously (Bange 1959). Epstein, Rains and Elzam (1963) confirm that two sites are available for potassium uptake and that only the one operating at high concentrations of potassium is affected by competition from sodium.

The existence of more than one site for the absorption of potassium, one of which is not subject to competition from other ions, probably explains the contradictory findings in relation to competition between potassium and magnesium. Whole plant studies indicate that competition is very likely at uptake, because in solution culture total plant magnesium is reduced in the presence of high potassium levels. However Omar and El Kobbia (1965) found that high magnesium in the medium did not reduce the amount of potassium in plants. This may be explained by the fact that not all potassium sites are subject to competition from magnesium while the effect of magnesium on those that are is masked by the ease of entry of potassium through the unaffected sites.

TRANSPORT OF IONS THROUGH PLANT TISSUES.

In general, similar considerations of transport between cells hold in both roots and leaves. Transport between cells in leaves has been studied in detail by Arisz and his associates (Arisz 1953; Arisz and Schreuder 1956; Arisz and Sol 1956).

The protoplasm of a multicellular organism is continuous between cells by way of plasmodesma or protoplasmic connections, forming a continuous body of protoplasm or "symplasm". It is through this symplasm that ions are transported from cell to cell (Arisz 1953; Arisz and Schreuder 1956; Arisz and Sol 1956). Experiments with metabolic inhibitors indicate that movement is through the cytoplasm and that diffusion through the cell wall is not involved (Arisz 1953). The cytoplasmic diffusion appears to be in the main, passive (Kramer 1957; Arisz 1958) but Bowling and Stanswick (1964) found that while potassium moved passively through root tissue, chlorine was moved actively against an electro-chemical gradient.

It appears likely that salts do not usually enter the cell vacuoles on their way to the xylem (Broyer 1950). Rather transport is direct through the cell protoplasm to the xylem vessels, bypassing the vacuole (Hodges and Vaadia 1964 a, b, c). On the other hand, the vacuoles seem to compete for available salts from the cytoplasm, and salts accummulated by them are not readily exchangeable with the symplasm region of the root (Crafts and Broyer 1938; Broyer 1950; Lundegardh 1950; Bowling and Weatherly 1964). Such salts are not necessarily unavailable to the rest of the plant. Under conditions of salt starvation, they may be released and transported elsewhere (Steward et al 1942).

Laties (1959) suggests that since salt concentration in the zylem often exceeds that of the external solution, the cytoplasm must be separated from the external solution by a diffusion barrier. If this was not the case there would be no way of retaining salts against diffusion loss to the environment. Sutcliffe (1962) points out that an effective barrier may be situated in the endodermis, as

as suggested long ago by Priestly (1920), where the Caspian bands prevent leakage of aqueous solution inwards or outwards along radial and transverse walls. Laties and Bud (1964) support the importance of the endodermis as the effective barrier. Such barriers are not however completely impermeable to the outward diffusion of all ions. When there is a net uptake of potassium, Mengel (1964) found that potassium was released by barley roots to the environment by what he assumed to be a process of a passive back diffusion through plant membranes. Cation accummulation had been considered to be irreversible (Epstein, Rains and Schmid 1962), however the eventual decrease in accummulation rate of potassium and sodium has been shown to be the result of an increasingly significant efflux of those ions (Jackson and Stief 1965). This has not been demonstrated for other ions, but similar behavior is likely.

Crafts and Broyer (1938) suggest that salts leak passively into the xylem and are not secreted into it, and this view is also held by Lundegardh (1955). A different situation is envisaged by Russell (1954) who suggests that secretion into the stele is similar to secretion into the cell vacuole (Russell and Sharrocks 1959). Evidence against the leakage hypothesis is not confined to the effect of such substances as D.N.P. (Randall and Vose 1963) and chloramphenicol (Uhler and Russell 1963) on the transport of ions to the xylem but is also supported by the stimulatory effect of respiratory substances on such transfers (Bange 1965).

THE EFFECT OF POTASSIUM ON PLANT MAGNESIUM AND ITS MOBILITY.

According to Hovland and Caldwell (1960):

1. Addition of potassium to a soil may decrease the ease of replacement of clay fraction magnesium and result in less magnesium being available for uptake.

2. Increased soil potassium may compete with magnesium at absorption sites on the plant roots and thus decrease magnesium uptake.

3. High amounts of potassium in plants may, in some way, prevent magnesium from performing all of its functions.

Soil magnesium is mainly contained in the silicate minerals, both primary and secondary. It may be substituted isomorphously in the octohedral layers of the crystal lattice or in inter-layer positions, depending on the type of clay (Salmon 1963). The clay fraction is likely to contain two-thirds of the soil magnesium with smaller amounts of magnesium in exchangeable and water soluble forms (Salmon 1963). Magnesium may also be held in unexchangeable forms by soil organic matter (Bould 1964).

The effect of potassium on the cation-activity ratios in equilibrium soil solutions has been studied on a range of soils (Hovland and Caldwell 1960; Shone 1967). With all soils increased potassium decreased the magnesium content of plants grown in them which was in turn correlated to a particular activity ratio in the soil solution (Hovland and Caldwell 1960; Adams and Henderson 1962; Salmon 1963, 1964). This effect was attributed to decreasing ease of release of magnesium from the soil clays in the presence of increasing amounts of potassium (Hovland and Caldwell 1960) and is particularly likely to occur with montmorillonite amounts (Hovland and Caldwell 1960). McLean (1949) studied cationic activity in the solution phase of clay suspensions and found that the activity of magnesium decreased rapidly with increased potassium saturation of a montmorillonite clay to the extent that it was unmeasureable when more than 5% of the clay's adsorption capacity was occupied by potassium

As little as 2½% saturation of the clay with K^+ caused a 10-fold drop in the activity of Mg compared with its activity at 100% saturation. In addition, he examined the behaviour of beidellite, halloysite and grundite illite and found that halloysite alone failed to show this depression of magnesium activity. In soils, Welte and Werner (1963) suggest that this effect is only apparent at low magnesium levels.

Observations of the effect of high soil potassium in reducing the magnesium content of leaves particularly of perennials, have been recorded over a long period. Osterhout (1907) apparently made the first such observation. Garner et al (1923) found a similar effect with tobacco, and Wallace (1925) with apples, currents and gooseberries. Many similar observations have been made on the effect of potassium on the uptake of magnesium from soils (e.g. Bower and Pierre 1944; Walsh and Clark 1945 a and b; Walsh and O'Donohue 1945; Bear and Prince 1945; Brown and Munsell 1956; Andrews 1960; Adams and Henderson 1962). These observations are difficult to interpret because they either do not examine the total magnesium taken up by the plant or they do not distinguish between the effect of potassium on the availability of magnesium from the soil on the one hand, and reduced uptake due to competition at the root or reduced translocation within the plant. Data which refer to leaf levels of magnesium only, may reflect a depression of the magnesium level in the whole plant, or a change in distribution of the element within the plant.

The inter-relationship has also been studied in culture solution, to avoid the soil effect, and many authors have determined the magnesium content of the whole plant. These experiments have provided evidence that potassium does reduce the amount of magnesium taken up (Scharrer and Mengel

1960; Komai 1963; Kloke 1964; Yoshida 1964; Schiedecker 1964; Madhok 1965; Omar and El Kobbia 1965; MacLeod and Carson 1966). On the other hand, Omar and El Kobbia (1965) produce evidence that high magnesium has no effect on potassium uptake by plants.

In contra-distinction, Cain (1948; 1953 a & b 1955) carried out intensive investigations on the effect of various levels of potassium on the uptake and transport of magnesium within apple plants, with very different results. He found that increasing the potassium in the medium caused increased growth and therefore some growth dilution , The translocation of magnesium from roots to tops was greatly reduced. Magnesium accumulated in the roots to such an extent that ultimately the absorption of magnesium ceased (Cain 1953, 1955). It appears that, with apples at least, the major effect is on the transport of magnesium within the plant. Perhaps in most plants, antagonism at the site of uptake and distribution within the plant are both affected by elevation of the level of potassium in the medium.

The mobility of magnesium within the plant has recently been subjected to question (Oland and Opland 1956; Neales 1958). Previously the fact that magnesium deficiency symptoms occurred first on the older leaves of a plant was taken to indicate that the element was very mobile within the plant and that when deficient was transferred from older leaves to younger leaves and growing points (Kidson 1946; Wallace 1951). The higher magnesium content of seeds was also taken as an indication of mobility (Williams 1955). Fudge (1938) related the susceptibility of citrus varieties to magnesium deficiency to the number of seeds they produced. He showed that seeds had a high magnesium content and in times of deficiency the magnesium content of nearby leaves was lowered. High diurnal

variations recorded in the magnesium levels in cotton (Phillis and Mason 1942) and apple leaves (Allen 1960) are also indicative of mobility of the nutrient. Benefit to magnesium deficient plants has resulted from spraying their foliage with a solution of magnesium sulphate) Boynton et al. 1943; Boynton 1945; Southwick and Smith 1945; Camp 1947; Fisher and Walker 1955; Walker and Fisher 1957; Forshey 1959). This indicates a certain mobility of magnesium under deficiency conditions. However, Oland and Opland (1956) could find no evidence that magnesium sulphate applied in this way could be transported to other parts of the plant. Bukovac and Wittwer (1957) and Bukovac et al. (1960) found that foliar applied Mg^{28} was immobile. Millikan and Hanger (1965) found that apparently immobile foliar doses of Ca^{45} became mobile when non-radioactive Ca^{++}, Mg^{++} or H^{+} was added to them. They related this effect to the ionic fixing capacity of the leaf which had to be saturated with Ca^{++}, Mg^{++} or H^{+} to free the tracer dose. A similar result may explain the apparent immobility of Mg^{28} found by Bukovac et al. (1960).

It is more difficult to explain the findings of Ruck and Gregory (1955) and Neales (1958) that there is no significant transfer of magnesium from older to younger leaves in potatoes and clovers respectively. However, Sucoff (1960) has produced evidence that young pine seedlings transfer magnesium from older to younger needles. Very early work of Dix and Bishoff (1930) and Deleano and Gotterbram (1936) with cereals suggested that magnesium moved from the stalk to the developing grain even though magnesium was still being taken up by the plant. Michael (1941) also found that magnesium of the lower leaves of oat plants could be redistributed to the developing inflorescence. Kidson (1946) found similar redistribution

in apples.

Although some confusion still exists, the weight of evidence suggests that magnesium is mobile within the plant. Cain (1948, 1953 a and b, 1955) has given one example of potassium interfering with this mobility. Examination of the importance of this mechanism in the production of potassium induced magnesium deficiency formed part of the present study.

111. MATERIALS AND METHODS.

A. INTRODUCTION.

The effect of potassium on the level of foliar magnesium has received much attention in the literature. Its effect on total plant magnesium has not received the same emphasis. Antagonism at the root surface, nutrient imbalance within the plant and the possible effect of potassium on translocation of magnesium within the plant, have received little attention.

The possibility of antagonism at the uptake site was investigated using the method of Epstein and Hagen (1952). This involved short term uptake for a period of 2½ hours using excised barley roots which were exposed to magnesium solutions with varying potassium content.

The effect of potassium on magnesium levels of plant organs in the absence of antagonism at the root was also investigated: firstly by applying potassium and magnesium to separate portions of a split root system and secondly by injection of potassium and magnesium into plant tissues.

Movement of magnesium between plant organs, when plants were subjected to magnesium free conditions, was studied on plants of different potassium status.

Onset of magnesium deficiency is related to the stage development. Deficiency symptoms often occur towards the end of the growing season, when demands by the fruit, and in particular the developing seed, increase greatly the plant's magnesium requirements. It was therefore decided to investigate the effect of varying potassium levels on magnesium distribution during the plant's development from seedling to maturity.

Plant material.

It was unavoidable that several species of test plants were used to suit the purpose of the different experiments.

In the short term uptake studies, barley was chosen because methods for its culture have been accurately worked out (Epstein and Hagen 1952) and because information on the uptake and antagonism of many other ions has been gathered using barley roots as experimental material.

Barley was used also in the studies of whole plant and development effects of potassium, to facilitate the use of information from the short term uptake experiments, in the interpretation of the whole plant experiments.

Barley was however, not suitable for the other experiments. Maize was chosen for the split root experiments because it was more susceptible to magnesium deficiency and displayed easily recognisable symptoms of the condition (Hambridge 1941), it quickly produced a strong root system which could be readily divided into two sections, and it may be grown successfully in a convenient flow culture apparatus (Sabet, Abdel Salam and Langerweff 1964).

Tomato was used for the experiments involving injections and transfer to magnesium free conditions, not only because this plant readily displays symptoms of potassium and magnesium deficiency, but also because it is more convenient for injection techniques, having the strong lateral beneath the first flowering truss which is a simple injection site. In addition, the plants are more easily dissected.

B. SHORT TERM UPTAKE METHODS.

A modification of the Epstein (1961) technique was used to produce sufficient low salt roots to provide material for magnesium analysis. The apparatus is illustrated in Plate 1.

Sixty grams of uniform barley seed (var. Proctor) were weighed out and surface sterilised in 10% hydrogen peroxide for 20 min. The seed was then enclosed in a butter-muslin "tea bag" fastened with terylene thread, and soaked in aerated distilled water for 24 hours. After this time, the bag was opened and spread over a plastic coated frame of perforated steel. This was made from $\frac{1}{8}$ in. perforated steel sheet, measured $11\frac{1}{2}$ x 10 ins. and was fitted with four $3\frac{1}{2}$ in. steel legs. The frame was completely coated with "Telco-thene" plastic.

The stand replaced the expensive stainless steel type used by Epstein. The frame was placed in a plastic container holding 6 litres of 5×10^{-4}M $CaSO_4$ solution, so that approximately 2 cm separated the seed and the solution surface. The butter-muslin was arranged so that its corners hung over the sides of the frame and dipped into the solution. The seed was then spread evenly over the cloth. A piece of plastic shade cloth which was used as an economical substitute for the stainless steel mesh suggested by Epstein, was placed over the seed and covered by a piece of butter-muslin, arranged as before (c.f. Epstein, Schmid and Rains 1963). Eight of these containers were set up in a darkened room maintained at 24° C. Each container was continuously aerated by a "Hi-flo" aquarium pump. Initially each container was aerated through two porous aeration blocks in each container. When it was noticed that roots grew poorly over some areas of the screen, the number of aeration points was increased to four in each container, and good even growth resulted.

PLATE 1.

Apparatus used for growing low salt roots for short term uptake studies.

The plastic vessel on the left shows the plastic-coated frame *in situ*, covered with butter-muslin on which the surface sterilised seed is placed. Turned back for viewing are the pieces of shade gauze and the second piece of butter-muslin, which cover the seed for the first 44 hours.

The vessel on the right contains barley seedlings 6 days old, immediately prior to root harvest. In front of this vessel is one of the plastic-coated, perforated steel frames, while on its right is one of the "Hi-flo" aquarium pumps which provided the aeration.

After 44 hours the top muslin and the shade cloth were removed. The calcium sulphate solution was renewed after 3 days. The roots were harvested on the 6th day. They were cut as closely as possible from the under surface of the screen with a pair of sharp scissors. The roots from all containers were placed in aerated 5×10^{-4} $CaSO_4$ solution and thoroughly mixed.

For the uptake experiments the procedure was that of Epstein, Schmid and Rains (1963). Containers were washed thoroughly and all solutions were allowed to equilibrate to constant temperature before use.

Three litres of the solution, from which uptake was to be measured, were placed in 9 pint black plastic buckets. Each vessel was aerated by means of a "Hi-flo" pump, so that lack of oxygen would not limit uptake (Hoagland and Broyer 1936, 1942).

Approximately 5 g of detached roots were placed on an 18 in. square of terylene gauze (openings approximately 1 mm) and thoroughly rinsed for 1 min. through each of two changes of de-ionised water. The edges of the gauze were brought together and tied with thread. The bag thus formed was whirled rapidly through the air by an attached thread to spin off surplus moisture.

The roots were then placed in the appropriate uptake solution. This was done by opening the bag and laying the gauze across the top of the vessel so that the centre carrying the roots, sagged into the solution. After 2 hours, the roots were removed by quickly lifting the gauze which was transferred to a stream of de-ionised water for 10 seconds (Lazaroff and Pitman 1966). At the end of the rinsing period, the neck of the bag was again closed and surplus water removed as before; the procedure being repeated at 4 minute intervals for all treatments.

Each experiment was designed as a 5 x 2 factorial in three replications requiring 30 uptake vessels in each experiment. Information was thus obtained from each experiment to plot four points on each of two lines (representing two levels of the interfering ion) control values being subtracted from the results to determine uptake figures in each case.

Roots were dried in an oven, with forced draft, at 75°C. The dried roots were ground in a glass mortar and stored in glass vials for chemical analysis.

C. SAND CULTURE METHODS.

Undrained, black plastic, 9 pint buckets were used as containers. The sand used was well graded local river sand, with a strong mode in the 2-3 mm size range, free of shell and of low clay content (Hewitt 1966). The clay was removed by several washings with tap water. The sand was then allowed to drain. Each container was filled with 2,800 g of well packed wet sand. Containers were watered daily to this weight with half strength Long Ashton Solution (Table 1.), as modified by Hewitt (1963). Iron was added to this solution as the ferric salt of potassium ethylenediaminetetra-acetic acid prepared as described by Jacobson (1951). A.R. grade chemicals and de-ionised water of low conductivity (less than 0.1 μ MHOS/cm) were used to make up the solutions, which were modified for each experiment in accord with the appropriate treatments.

The sand cultures were grown in a ventilated glasshouse, heated during the winter months. Each treatment was replicated and randomised according to experimental design.

TABLE 1.

Long Ashton Nutrient Solution (Hewitt 1963)

Salt	g/l	ppm
KNO_3	0.505	K, 195; N, 70
$Ca(NO_3)_2$	0.820	Ca, 200; N , 140
$Na\ H_2\ PO_4.2H_2O$	0.208	P, 41
$MgSO_4.\ 7H_2O$	0.369	Mg, 36
Fe - EDTA		Fe, 2.8
$Mn\ SO_4$	0.00223	Mn, 0.55
$CuSO_4.\ 5H_2O$	0.000240	Cu, 0.064
$Zn\ SO_4.\ 7\ H_2O$	0.000296	Zn, 0.065
H_3BO_3	0.00186	B, 0.37
$(NH_4)_6\ Mo_7O_{24}.4H_2O$	0.000035	Mo, 0.019
$CoSO_4.\ 7\ H_2O$	0.000028	Co, 0.006
Na Cl	0.00585	Cl, 3.55

D. SOLUTION CULTURE METHODS.

Black, 9 pint, plastic buckets, which had been coated with aluminium paint to reduce heat absorption were used as containers. The top of each container was fitted with a disc of $\frac{1}{4}$ in. black polyvinyl plastic, which was provided with a central hole for an aeration tube and two $\frac{3}{4}$ in. holes, situated opposite each other, half way along the disc radius. Each hole was fitted with an inch long piece of black plastic electrical conduit, the bottom end of which was crossed at right angles by two plastic tooth picks to form a convenient plant holder (c.f. Hewitt 1966). The disc was covered with aluminium foil to reduce heating of the nutrient solution. The solution culture apparatus, in process of assembly, is illustrated in Plate 2.

A small seedling, raised in sand, was carefully washed and supported in each holder by means of a plug of crimped "Terrylene" fibre (Fibremakers Ltd., Bayswater, Victoria), which is the nearest local equivalent to the fibre suggested by Hewitt (1966).

Each container was filled with $4\frac{1}{2}$ litres of the nutrient solution described in Table 1 or a modification of it to provide the required treatment levels of magnesium or potassium. The solutions were aerated continuously through a glass tube supported in the central hole, by means of a "Hi-flo" aquarium pump. Each solution was renewed weekly.

E. SPLIT ROOT METHODS.

Sabet, Abdel Salam and Lagerweff (1964) described a narrow chamber which they used to study the effect of nutrient solution flow rates on the growth of plants. A number of these containers was made in duplex but otherwise to their specifications. The duplex container, which is shown diagrama tically in Figure 2, consists of two chambers

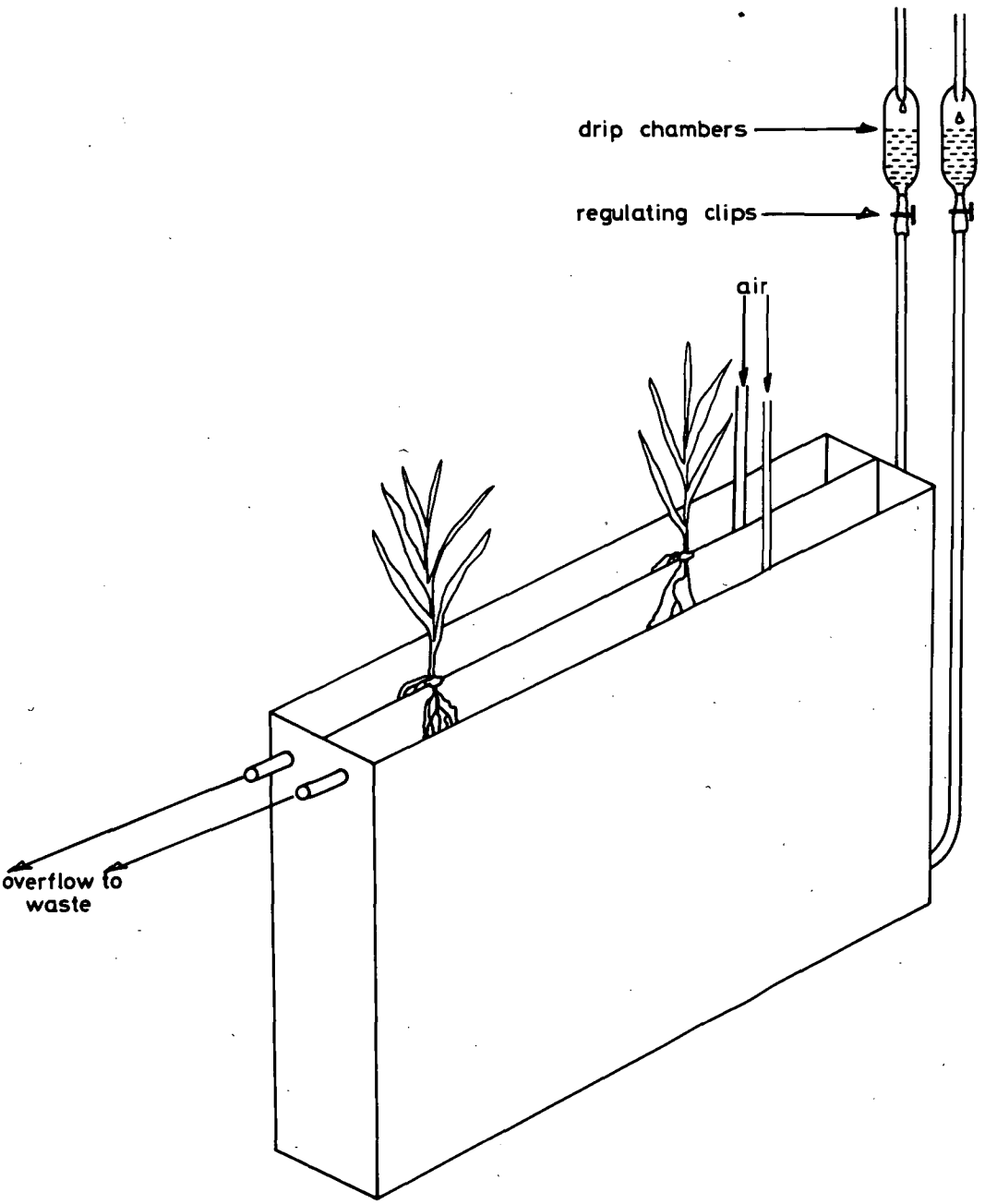
PLATE 2.

Containers used in solution culture experiments, in the process of assembly.

Each container was coated with aluminium paint, and each supporting disc covered with aluminium foil, to reduce absorption by the nutrient solutions. Each container was aerated from the "Hi-flo" pump seen towards the rear, through the red plastic tubes.
In front can be seen the plastic supporting discs, fitted with 1 in. of black plastic electrical conduit to form a plant holder which is closed off at the bottom by two coloured plastic tooth-picks.

FIGURE 2.

Culture chamber used in split root experiments.


drip chambers
regulating clips
air
overflow to waste

each measuring $9\frac{1}{2}$ x 7 x $\frac{3}{4}$ in. Nutrient solution enters near the bottom of one end of each chamber and flows out near the top of the opposite end. Rate of flow from an elevated reservoir was regulated by a blood transfusion drop chamber and a Hoffman clip. The solution was aerated through a glass tube placed at the entry end of the chamber. An enamelled wooden cover, with four centrally placed holes, supported the plants in the chambers. Plate 3 shows the apparatus as set up in the glasshouse. The nutrient solution given in Table 1 was modified to meet treatment requirements and was supplied to each chamber at a flow rate of 8 l./hr. (Sabet, Abdel Salam and Lagerweff 1964).

Young maize seedlings (var. Golden Cross Bantam) at the third leaf stage, were carefully lifted from the sand in which they were raised. The roots were carefully washed and the central tap-root removed. These plants were held with "Terrylene" fibre in the holes of the wooden covers. As each cover was placed in position, half the roots of each plant were distributed to each chamber.

F. METHODS OF CHEMICAL ANALYSIS.

Drying plant material: Harvested plant material was dried at 75°C in an oven with forced draft. Small samples were then ground in a glass mortar and the larger ones in a small "Culatti" hammer-mill. The mill was thoroughly cleaned with compressed air between samples.

Digestion of samples: Either 0.1 or 0.2 g of finely ground, oven dried plant material was weighed out into "Pyrex" test tubes. These samples were digested with 5 ml of acid mixture (1 volume 70 % perchloric acid plus 5 volumes 70 % nitric acid), by heating the test tubes

in an aluminium block on a hot plate. The block was milled from a piece of aluminium to 14 x $4\frac{1}{2}$ x $3\frac{1}{2}$ in. size. It contained 24 holes 2 in. deep and of $\frac{3}{4}$ in. diameter in which the tubes stood during digestion. When digestion was completed, the digestate was made up to 20 ml with distilled water and thoroughly mixed.

Sodium and potassium: 5ml of this solution was diluted to 25 ml with distilled water and the concentration of the metals in the resulting solution was measured with an E. E. L. flame photometer (Vogel 1962).

Calcium and magnesium: A further 5 ml of the same solution was diluted to 25 ml with a solution of strontium chloride and isopropanol so that the final solution contained 1500 ppm strontium and 10 % isopropanol. Strontium has been found to minimise interference by phosphate (Parker 1963) and isopropanol has been shown to give increased sensitivity in atomic absorption spectrophotometry (Allan 1961; Gibson et al. 1963). Calcium absorption at 4227 Å and magnesium absorption at 2852 Å was measured using a "Techtron" AA-100 atomic absorption spectrophotometer (Allan 1958).

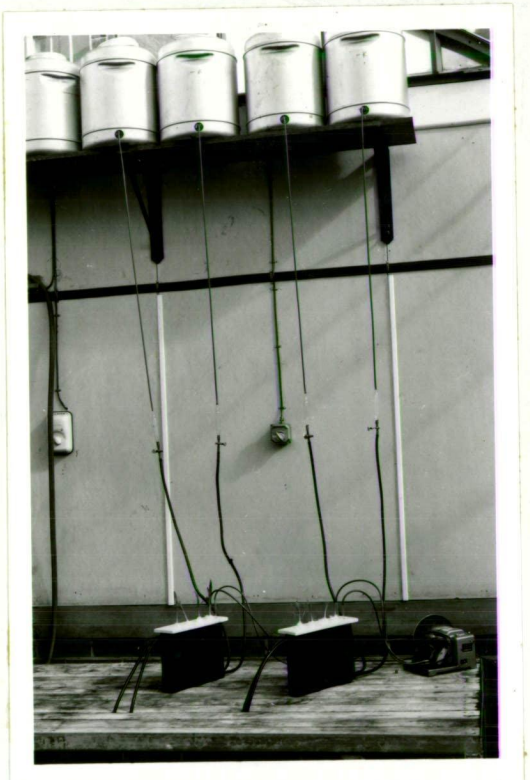
Phosphorus: This element was determined by the molybdo-vanadate method (Jacob and Hoffman 1954). One gram of ammonium metavanadate was heated with a mixture of 300 ml water and 200 ml concentrated nitric acid until dissolved. This was added to 40 g of finely ground ammonium molybdate dissolved in 400 ml of warm water. The resulting solution was made up to one litre.

A 5 ml portion of test solution was taken and to it was added 5 ml of molybdo-vanadate reagent. The combined solution was diluted to 25 ml, thoroughly mixed, and the resulting yellow colour measured after 30 minutes on a Bausch and Lomb "Spectronic" spectrophotometer at 400 mμ.

PLATE 3.

Split root apparatus as set up in the glasshouse.

The elevated plastic drums, which acted as reservoirs, were coated with aluminium paint to help reduce heating of the nutrient solution. Opaque plastic tubing was used to prevent algal growth. Glass dropper tubes were covered with aluminium foil, except when drip rate was being adjusted, for the same reason.



1V EXPERIMENTAL

1. Potassium - magnesium antagonism at uptake.

(a) The effect of potassium on the uptake of magnesium.

Solutions contained 0, 2.5, 4.0, 7.5 and 15 mM $MgCl_2$. These levels were chosen on the basis of the findings of Lazaroff and Pitman (1966). The two levels of potassium chloride used were 0 and 25 mM KCl. The rate of uptake of magnesium by the roots was calculated as μ mol/g/hr and plotted against $MgCl_2$ concentration for each level of KCl, Figure 3. The data were also expressed in a double reciprocal plot (Figure 4), after Lineweaver and Burk (1934). The straight lines which were obtained indicate that the application of Michaelis-Menten enzyme kinetics to the data is appropriate.

In the presence of potassium ion, the slope of the line was increased (reduced Mg uptake) but the intercept, 1/V, remained constant at 0.16, equivalent to a maximum velocity, V, of 62.5 μ mol/g/hr. In confirmation of this result, a second experiment was carried out with identical treatments and design except that the concentration of potassium ion was reduced to 10 mM KCl. The results obtained are also shown in Figure 4. The base line (solid dots) obtained in the absence of potassium was identical with that obtained in the first experiment.

(b) The effect of magnesium ion on the uptake of potassium.

Solutions contained 0, 5, 7.5, 10 and 25 mM KCl. The two levels of magnesium chloride used were 0 and 25 mM $MgCl_2$, the upper level being greater than levels used in the initial experiment to ensure an effect. The rates of uptake of potassium, calculated as μ mol/g/hr and plotted as before, are shown in Figure 5. The line obtained in the presence of magnesium is below the base line obtained in its absence,

FIGURE 3. (above)

Rate of Mg uptake as a function of the concentration of $MgCl_2$. Uptake measured in the presence of 0, 10 and 25 mM KCl.

FIGURE 4. (below)

Lineweaver-Burk plot of Mg uptake in the presence of 0, 10 and 25 mM KCl.

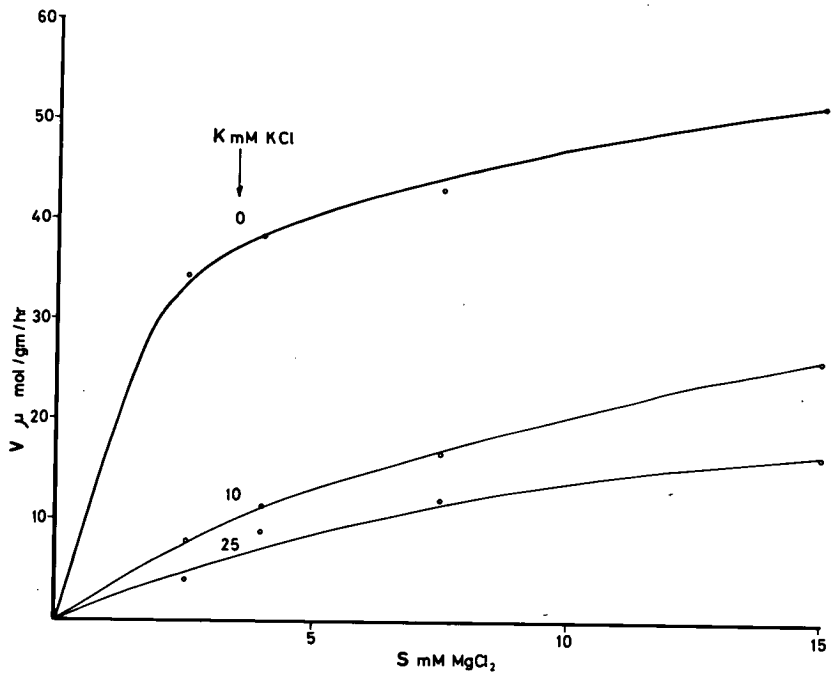
The following values were determined from the graph:

$1/V = 0.16$ $\quad V = 62.5$ μ mol/g/hr

$K_s = 2.4$ mM

$K_i(25) = 41.7$ mM

$K_i(10) = 17.2$ mM


60
50
40
30
20
10
V μ mol/gm/hr
K mM KCl
0
10
25
5
10
15
S mM MgCl2

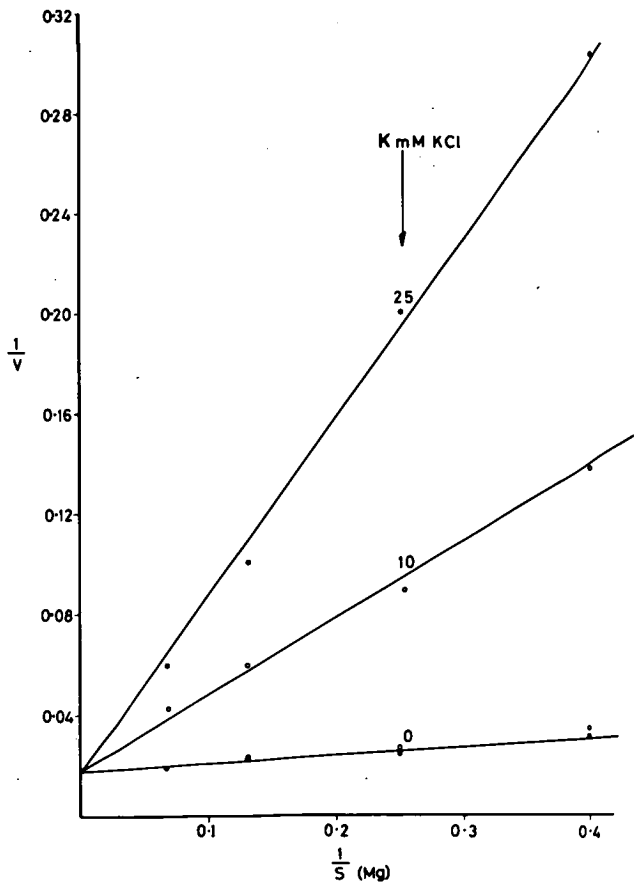
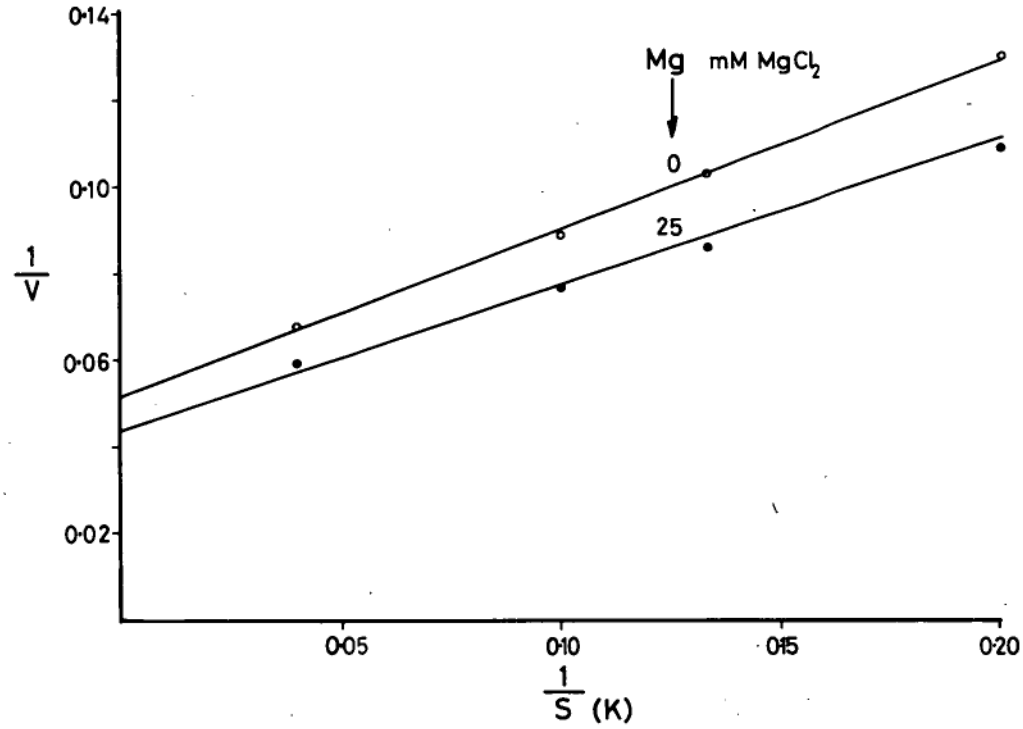

0·32
0·28
0·24
0·20
0·16
0·12
0·08
0·04
1/V
K mM KCl
25
10
0
0·1
0·2
0·3
0·4
1/S (Mg)

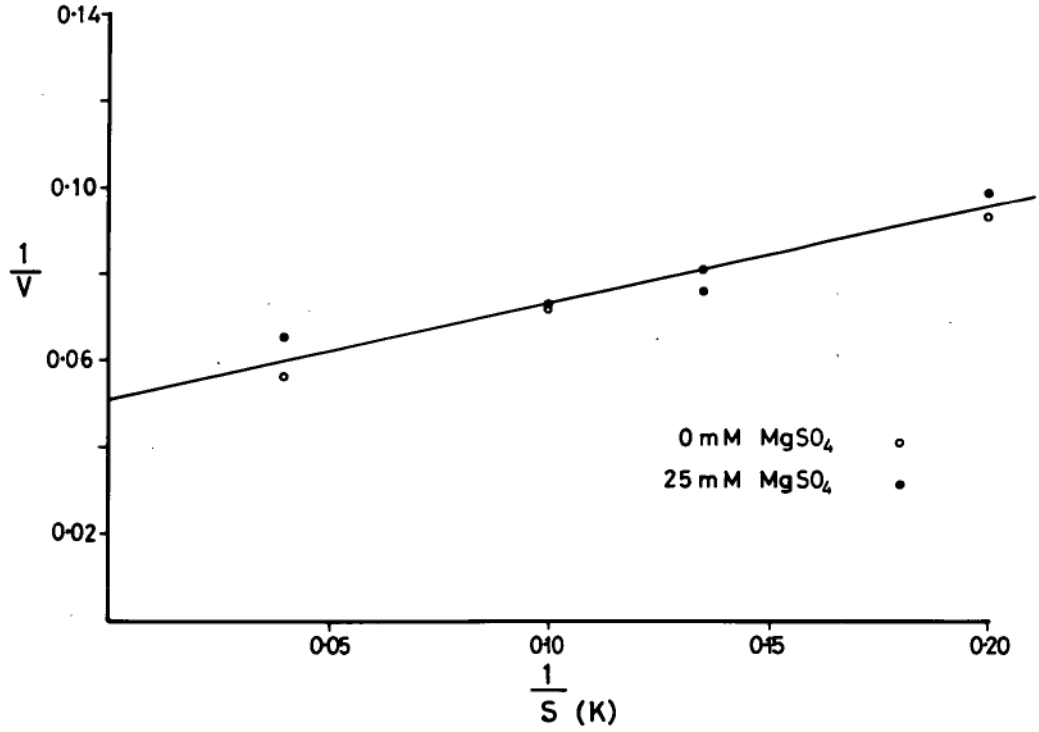
FIGURE 5. (above)

Lineweaver-Burk plot of K uptake by detached barley roots in the presence and absence of 25 mM $MgCl_2$.

FIGURE 6. (below)

Lineweaver-Burk plot of K uptake by detached barley roots in the presence and absence of 25 mM Mg SO_4.


0·14
0·10
0·06
0·02
1/V
Mg mM MgCl2
0
25
0·05
0·10
0·15
0·20
1/S (K)


0·14
0·10
0·06
0·02
1/V
0 mM MgSO4
25 mM MgSO4
0·05
0·10
0·15
0·20
1/S (K)

indicating an apparent stimulation of potassium uptake by magnesium, by chloride or by magnesium chloride salt. The effect was confirmed in a repetition of this experiment. (Appendix A).

(c) The effect of magnesium on potassium uptake when salts of different anions are present.

Solutions contained 0, 5, 7.5, 10 and 25 mM KCl. The two levels of magnesium were supplied as 0 and 25 mM $MgSO_4$. The rates of uptake in μ mol/g/hr are shown in Figure 6. The drawn line represents uptake in the absence of magnesium salt. Uptake in the presence of magnesium sulphate is shown by solid dots. It is clear that, in the absence of a common anion, magnesium had no effect on the uptake of potassium.

(d) Uptake of magnesium by barley seedlings in the presence and absence of potassium, compared with uptake by detached roots.

It was found in previous uptake experiments that each container used to produce low salt roots, yielded approximately 20 g of root material. In this experiment each container held four smaller plastic grids, supported above the $5 \times 10^{-4} CaSO_4$ solution by glass holders. Each grid was set up in the same manner as in previous experiments with butter-muslin and plastic shade cloth, each unit receiving 15 g of surface sterilized barley seed, making 60 g per container as before.

After six days the plants were used for a 2 hr uptake experiment. Solutions used were the same as for the first experiment using detached roots, namely, 0, 2.5, 4.0, 7.5, and 15 mM $MgCl_2$ and 0 and 25 mM KCl.

Each grid of plants was removed from the calcium sulphate solution and washed in two portions of de-ionised water. The grid was then shaken vigorously to remove as much water as possible. A grid was suspended by plastic coated bell wire over the appropriate uptake solution in such a way that only the roots were in the vigorously aerated solution.

The grid was removed after the 2 hr. uptake period and the roots washed through slowly running de-ionised water for 10 seconds. The grid was then inverted and tapped sharply to remove ungerminated barley seeds. The roots were removed with sharp scissors just below the plastic grid. The coleoptiles were then harvested as close to the seed as possible. Finally, the seeds plus a small amount of root and coleoptile were removed from the muslin. All samples were oven dried and analysed for magnesium.

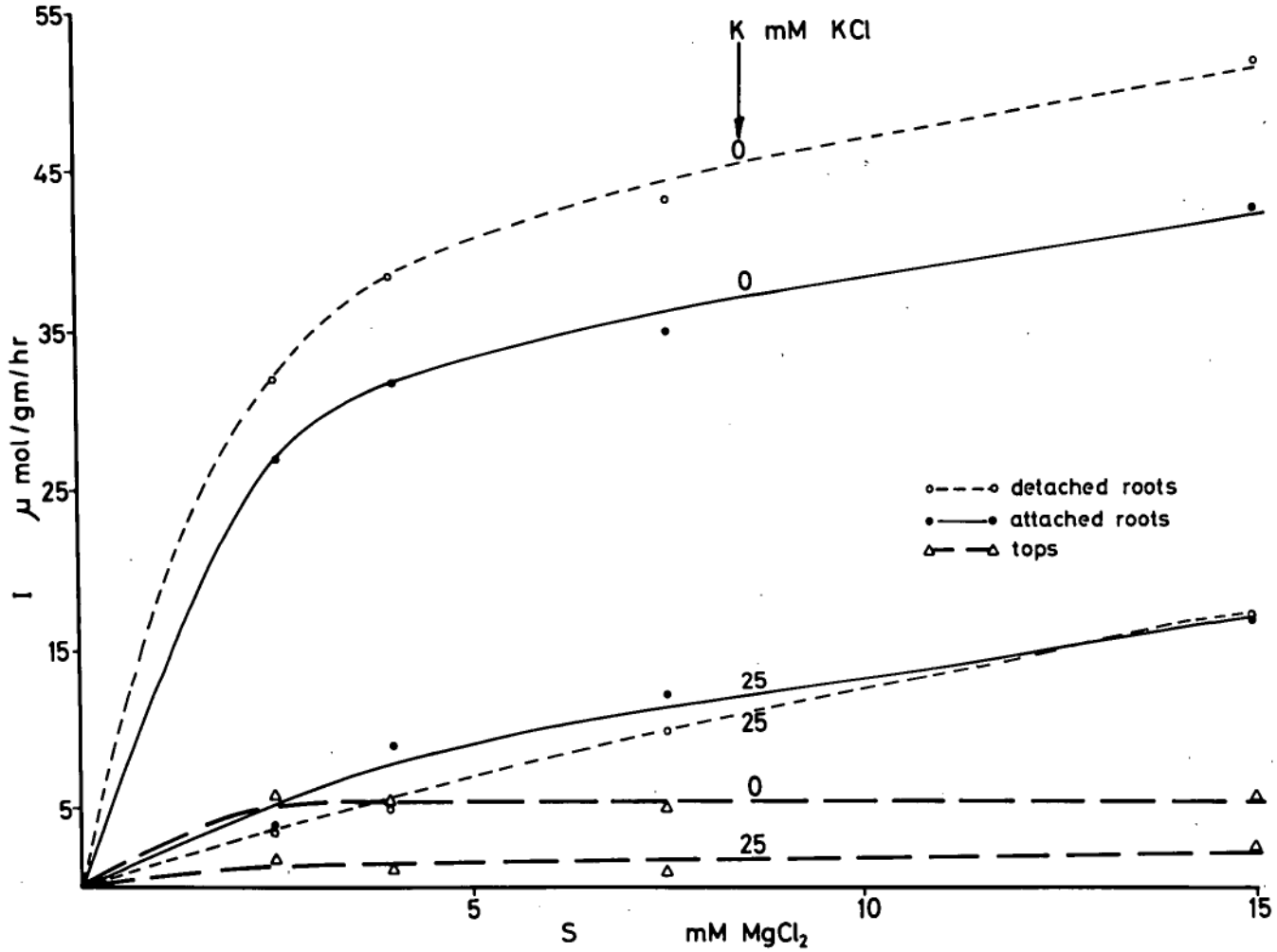
In Figure 7 the results of this experiment are compared with those of the first experiment, with detached roots.

Over the two hour period, attached roots took up magnesium from the solution and also transferred magnesium to the plant top. Both experiments were conducted under identical conditions and in Figure 7, net influx of magnesium for attached and detached roots has been compared both with and without potassium.

In the absence of potassium there is less net influx of magnesium into attached roots than into detached roots. This difference is due to the presence of the tops which act as a sink for magnesium: if the amount of magnesium taken up by the tops in the absence of potassium is added to the attached root uptake this difference in net influx disappears (Table 7), and total plant influx is about equal to detached root influx.

FIGURE 7.

Net influx of magnesium into detached and attached barley roots and into plant tops in the presence and absence of 25 mM KCl.


K mM KCl
0
0
25
25
0
25
detached roots
attached roots
tops
I μ mol/gm/hr
55
45
35
25
15
5
5
10
15
S mM MgCl2

In the presence of potassium the net influx of both attached and detached roots is decreased as would be expected with competition between potassium and magnesium at uptake. In addition, there is little difference between the net influx of magnesium into attached and detached roots. This could be due to either attached roots taking up more magnesium in the presence of potassium than might have been expected from their behaviour in its absence, or to a reduction in the amount of magnesium translocated to the tops. There is less magnesium in the plant tops in the presence of potassium but this represents about the same proportion of root magnesium as is present in the tops of the no potassium treatment.

(e) Effect of urea on magnesium uptake by detached barley roots.

Some evidence has been reported (Hafkenscheid and Bonting 1968) that urea inactivates an ATPase which participates in magnesium uptake by microorganisms. Magnesium solutions used in the experiment to test the action of urea on roots contained 0, 2.5, 4.0, 7.5, and 15.0 mM $MgCl_2$, while the two levels of urea used were 0 and 0.2 M urea. Solution pH varied between 6.6 and 6.8, a range over which ion uptake is not measurably affected (Epstein, Rains and Elzam 1963).

Uptake by excised barley roots was measured as μ mol/g/hr and plotted conventionally (Figure 8) and as a double reciprocal plot (Figure 9). Urea did not affect the uptake of magnesium by excised barley roots.

2. Potassium and magnesium uptake in the absence of competition at uptake.

(a) The effect of applying potassium and magnesium to separate parts of a split root system.

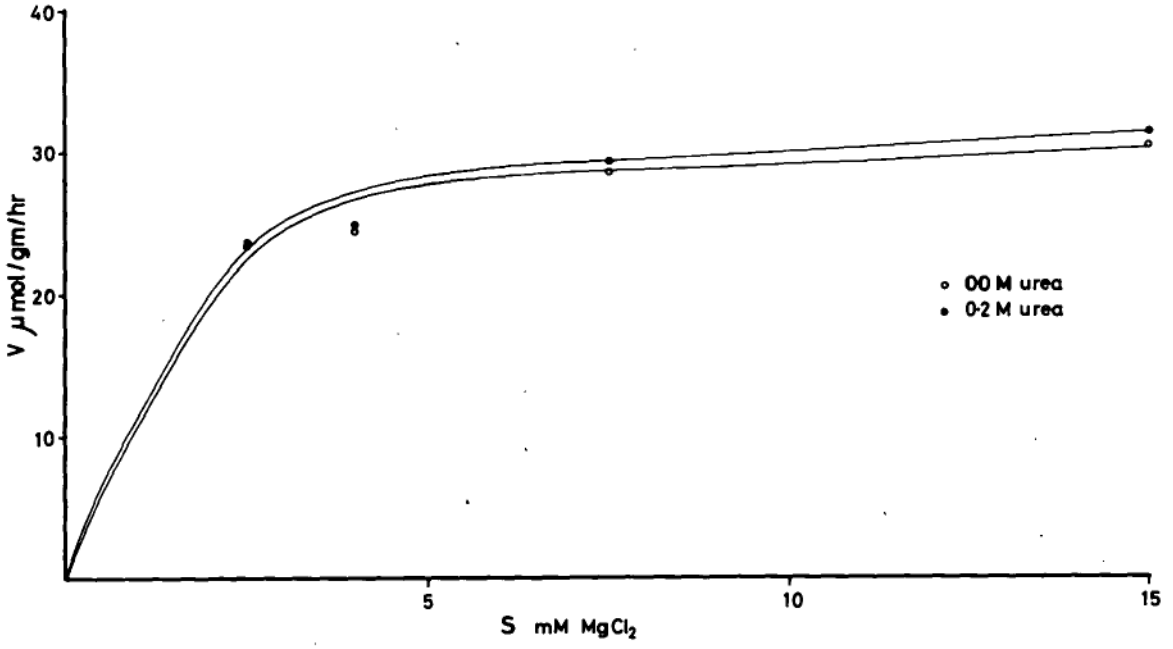
Solutions used were based on the Long Ashton solution (Table 1) which was modified to produce the five solutions in Table 2. These were run through chambers of the duplex

FIGURE 8. (above)

Rate of Mg uptake by detached barley roots as a function of the concentration of $MgCl_2$, in the presence and absence of 0.2 M urea.

FIGURE 9. (below)

Lineweaver-Burk plot of Mg uptake by detached barley roots in the presence and absence of 0.2 urea.


40
30
20
10
V μmol/gm/hr
5
10
15
S mM MgCl2
0·0 M urea
0·2 M urea

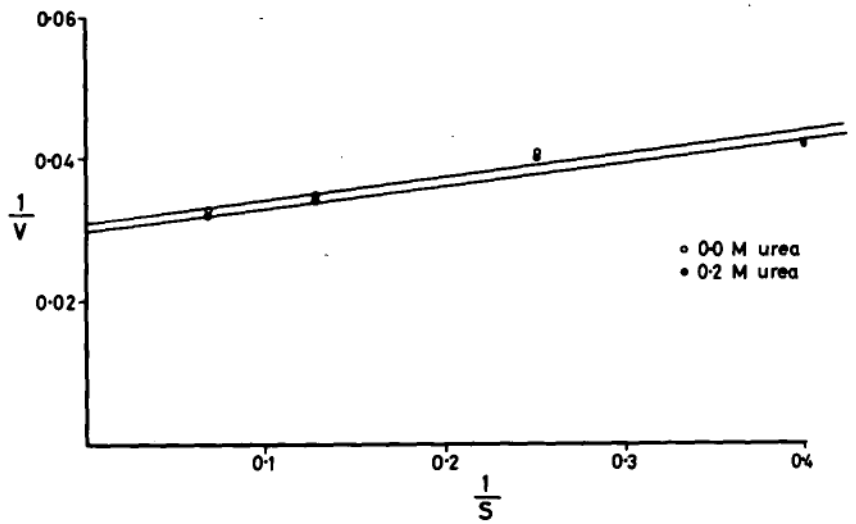

0·06
0·04
0·02
1/V
0·1
0·2
0·3
0·4
1/S
0·0 M urea
0·2 M urea

TABLE 2

Solutions for split root - flow culture experiment

Element	Soln. 1 ppm	Soln. 2 ppm	Soln. 3 ppm	Soln. 4 ppm	Soln. 5 ppm
K	195	390	390	-	-
Mg	24	4	-	4	24
Ca	200	200	200	200	200
N	210	210	210	210	210
P	41	41	41	41	41
Fe	5.6	5.6	5.6	5.6	5.6
Mn	0.55	0.55	0.55	0.55	0.55
Cu	0.064	0.064	0.064	0.064	0.064
Zn	0.065	0.065	0.065	0.065	0.065
B	0.37	0.37	0.37	0.37	0.37
Mo	0.019	0.019	0.019	0.019	0.019
Co	0.006	0.006	0.006	0.006	0.006
Cl	3.55	3.55	3.55	3.55	3.55

Solution 1. Control - Long Ashton

2. High K, low Mg

3. High K, No Mg

4. Low Mg, No K

5. Normal Mg, No K

containers (Figure 2) to produce combinations for the following treatments:

	Left Chamber	Right Chamber
Treatment 1/1	solution 1	solution 1
Treatment 2/2	solution 2	solution 2
Treatment 3/4	solution 3	solution 4
Treatment 3/5	solution 3	solution 5

Each solution was diluted to half strength. The experiment was carried out in duplicate over a period of 20 days. Because only eight duplex containers could be controlled and supplied with nutrient at the one time, only four treatments could be selected. Treatment 1/1 was the control. Treatments 2/2 and 3/4 were selected to examine magnesium uptake when potassium and magnesium were applied to separate parts of the root system. Treatment 3/5 was included to see if spatial separation of the nutrients would allow uptake of normal magnesium levels. Results are given in Table 3. Good agreement existed between duplicates of the experiment which was not subjected to analysis of variance (Appendix B).

When potassium was applied to the root system together with magnesium (treatment 2/2), the same amount of magnesium was taken up by the plants (0.921 mg) as was taken up (in treatment 3/4) when they were applied to different halves of the root system (1.138 mg). Both these treatments produced tops with a depressed magnesium content (0.284 % and 0.297 % respectively) compared with the control (0.673 %), and conspicuous symptoms of magnesium deficiency were displayed (Plate 4).

Potassium is generally believed to be readily redistributed within the plant and it is obvious in this experiment that potassium taken up by the roots to which it was applied, was distributed to the roots on the other side of the duplex chamber. Roots on the "no-potassium" side of the duplex

TABLE 3

Split Root Experiment

Distribution of potassium and magnesium in roots and tops

Treatment	Plant Part	Dry Wt. (g)	Mg %	Mg (mg)		K %	K (mg)	
1/1	Top	0.193	0.673		1.299	2.77		5.35
	root L.	0.042	0.253	0.106		5.71	2.40	
	root R.	0.091	0.344	0.313		4.16	3.79	
	Total				0.419			6.19
TOTAL PLANT					1.718			11.54
2/2	Top	0.216	0.284		0.613	2.18		4.71
	root L.	0.126	0.195	0.245		6.44	8.11	
	root R.	0.075	0.084	0.063		3.85	2.89	
	Total				0.308			11.00
TOTAL PLANT					0.921			15.71
3/4	Top	0.156	0.297		0.463	1.54		
	root L.	0.080	0.089	0.071		2.87	2.30	
	root R.	0.251	0.241	0.604		2.27	5.70	
	Total				0.675			8.00
TOTAL PLANT					1.138			10.400
3/5	Top	0.193	0.618		1.192	1.82		3.700
	root L.	0.063	0.205	0.129		2.34	1.47	
	root R.	0.107	0.666	0.712		4.38	4.69	
	Total				0.841			6.16
TOTAL PLANT					2.033			9.86

chambers contained 2.27 and 4.38 % potassium indicating that, contrary to the findings of Davidson (1944) with peach roots, potassium can be transferred from one part of the root system to another.

Analysis of the solution coming from the "no-potassium" chamber, 10 days after the start of the experiment, showed a potassium content of approximately 10 ppm. Simultaneous efflux and influx of root potassium has been demonstrated (Mengel 1964; Jackson and Stief 1965), and in this experiment it appears that potassium not only migrated from one side of the root system to the other but was also lost from the roots of the "no-potassium" chamber to the surrounding solution. Thus, in this experiment potassium was still capable of competing with magnesium at uptake on the "no-potassium" side. Even before potassium had reached any significant concentration in the solution on this side, it could well be that all the magnesium transporting sites were saturated with potassium to the detriment of magnesium absorption.

In addition, in both treatments 3/4 and 3/5 the roots in the chamber which received no magnesium (solution 3) had a lower dry matter production and a lower percentage magnesium content than the roots in the opposite chamber which received no potassium (solution 4 or 5). The "no-potassium" roots had a normal white appearance and a brittle texture. Roots in the "no-magnesium" chamber of treatment 3/5 showed a brown discoloration, were often covered with a gelatinous coat and were not as brittle as the roots in the "no-potassium" side. Roots on the healthy "no-potassium" side contained adequate potassium (2.27%), while roots on the "no-magnesium" side in this treatment, had a low magnesium content (0.089 %), which may account for their unhealthy appearance. This indicates that K may be redistributed to the deficient side. Since Mg

PLATE 4.

Magnesium deficiency of maize plants at time of harvest of the split root experiment.

The two groups of leaves on the left, showing severe magnesium deficiency, were taken from plants in treatment 3/4 where one side of the root system was supplied with high potassium levels and the other with low magnesium.

The two groups on the right, showing less severe magnesium deficiency were taken from plants in treatment 3/5, where one side of the root system received high potassium and the other side normal magnesium.

deficiency could not be overcome in this way, it might be assumed that magnesium is less mobile than potassium.

There is also some evidence that, in the presence of high potassium (treatment 3/5), more of the plant magnesium (0.841 mg) accumulated in the roots than was the case in the control (1/1) treatment (0.419 mg). Although magnesium is less mobile than potassium, the higher level of magnesium accumulated in the "normal magnesium" side (solution 5) of this treatment (0.666 %) apparently allowed a substantial level of magnesium (0.205 %) to be achieved from redistribution to the "no-magnesium" side. This was higher than the equivalent side in treatment 3/4 (0.08 %) and probably accounts for the healthier appearance of the "no-magnesium" roots in the high potassium treatment.

(b) The effect of applying potassium and magnesium by injection into plant tops.

Tomatoes (var. Grosse Lisse) were grown in sand culture as described earlier (page 48). Treatment levels of potassium and magnesium were provided by watering with nutrient solutions described in Table 4 diluted to half strength. Thirty-six cultures were set up, 18 being grown at normal nutrient levels (solution 1) and 18 at high potassium levels (solution 2), until each plant had produced a strong lateral. Grosse Lisse produces such a lateral just below the first fruiting truss.

This lateral was used for the introduction of injection solutions. Various methods of introduction have been described (Roach 1939; Roach and Roberts 1945). In a pilot experiment, injection through the petiole of a lower leaf was attempted. Almost invariably the petiole abscissed before much solution was taken up. For this reason entry through the lateral was used in subsequent work. It was found that large volumes of solution could be introduced into tomato plants in this manner(Figure 10). One of the

TABLE 4

Nutrient solutions for injection experiment

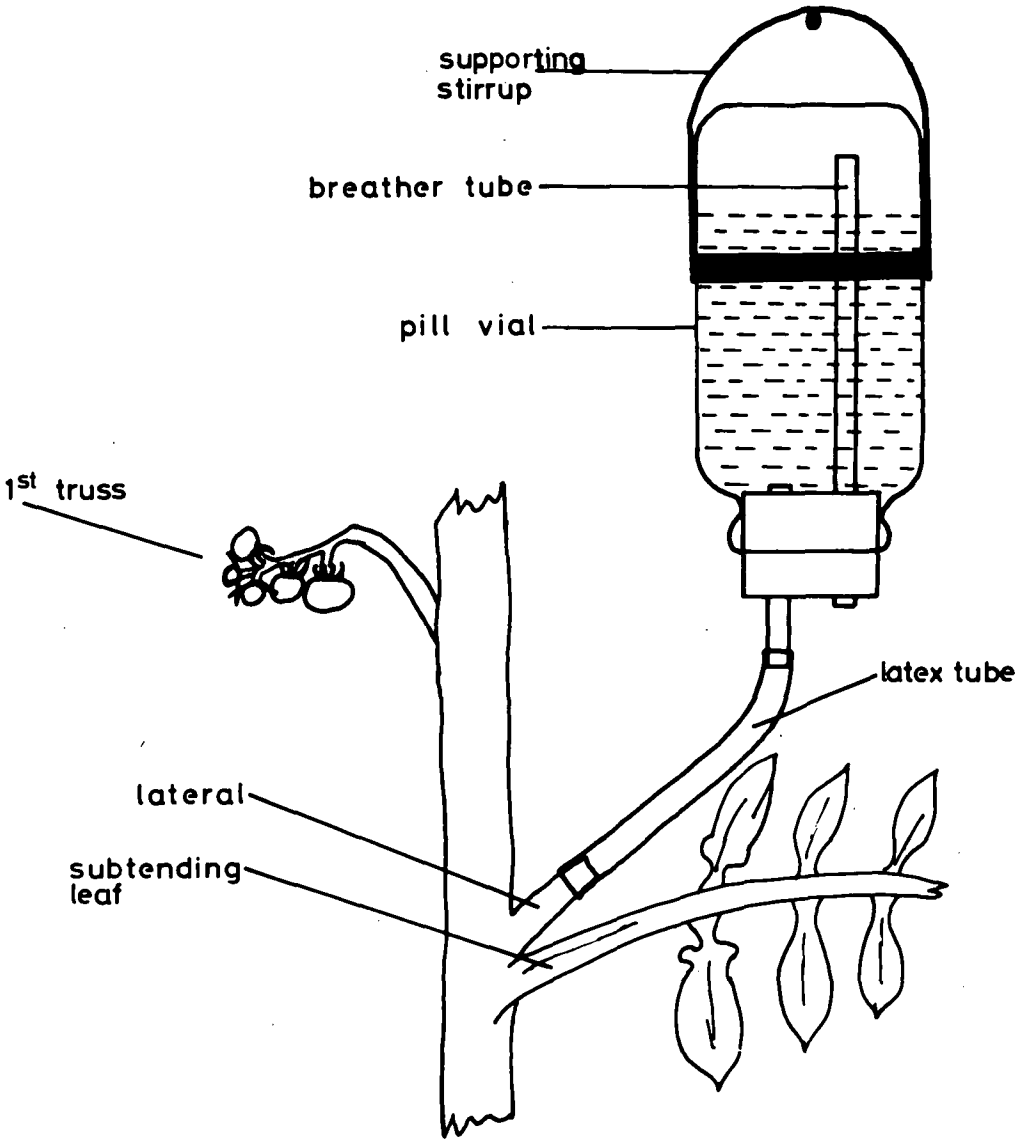
Element	Soln. 1 Control ppm	Soln. 2 High K ppm	Soln. 3 High Mg ppm	Soln. 4 High K & Mg ppm
K	195	390	195	390
Mg	24	24	48	48
Ca	200	200	200	200
N	210	210	210	210
Fe	5.6	5.6	5.6	5.6
Mn	0.55	0.55	0.55	0.55
Cu	0.064	0.064	0.064	0.064
Zn	0.065	0.065	0.065	0.065
B	0.37	0.37	0.37	0.37
Mo	0.019	0.019	0.019	0.019
Co	0.006	0.006	0.006	0.006
Cl	3.55	3.55	3.55	3.55

PLATE 5.

Tomato plant being injected through the stump of the lateral.

FIGURE 10.

Diagramatic representation of apparatus used for injecting nutrients into the cut lateral of tomato plants.


supporting stirrup
breather tube
pill vial
1st truss
latex tube
lateral
subtending leaf

injected plants is shown in Plate 5 soon after the beginning of an experiment.

An inverted pill vial, closed by a rubber stopper into which was fitted a glass outlet and a breather tube, was used to dispense 50 ml of the injection solution. A piece of soft, translucent, latex tubing attached to the outlet tube was pinched off after inversion to prevent the vial from emptyin g. The plant lateral was cut off with a sharp knife approximately 1 in. from the main stem. The latex tubing was quickly slipped over the stump and all bubbles, clearly visible through the latex, were removed from the system. Three plants from each treatment were rejected because their laterals were underdeveloped and this may have caused their rate of uptake to be slower. Fifteen plants at each level of potassium were available for injection.

Treatments were applied in a 2 x 5 factorial design with three replications, as follows:

NUTRIENT SOLUTION	INJECTION SOLUTION
	I_1, distilled water (control)
	I_2, 0.5 % $MgCl_2$ followed by
K_1, 195 ppm K, 24ppm Mg	I_3, 0.5 % Mg Cl_2 1 % KCl
K_2, 390 ppm K, 24 ppm Mg	I_4, 1 % KCl
	I_5, 48 ppm Mg applied to roots

In addition to the control, treatment I_5 was injected with 50 ml distilled water through the laterals. The magnesium level in this treatment was achieved by applying solutions 3 and 4 (Table 4) to plants which had been grown in solutions 1 and 2 respectively. In this way their previous nutrient status was maintained except for the increased level of magnesium and its complementary anion. Concentrations of potassium and magnesium used in the injections were based on those described as safe by Roach and Roberts (1945).

Absorption of solutions ceased after 10 days when 20-50 ml of solution had been absorbed. This effect was due to the occlusion of the vascular tissue. Differences in the amount of ion absorbed into the plants caused considerable variation between replicates. Mean values for Mg and K in the subtending leaves are given in Table 5.

Symptoms were first noticed three days after injection, and were very obvious on the 4th day. Injection of potassium was followed by the appearance of symptoms typical of magnesium deficiency, distributed in the same orthostichy above the point of injection. Injection of magnesium produced symptoms typical of potassium deficiency, distributed in like manner. Symptom distribution is illustrated diagramatically in Figure 11.

Symptoms of magnesium deficiency were not exactly as illustrated by Wallace (1951, plate 255) namely central intervenal chlorosis and green marginal bands. The leaf symptoms observed were intervenal chlorosis and necrosis, with green veins and to a lesser extent, green margins. Leaf appearance was thus more like that of the magnesium deficient plant illustrated by Wallace (1951, plate 257).

Symptoms indicative of potassium deficiency were slight marginal and intervenal chlorosis on leaflets followed by brown scorching of the margins, which curled forward. They were identical with the illustration and description given by Wallace (1951, plate 258).

Table 5 shows the mean potassium and magnesium contents of the leaves subtending the injected lateral and the symptoms displayed by them. Where the injection of magnesium was followed by potassium, the potassium deficiency symptoms induced by the initial magnesium injection remained although subsequent potassium injection raised the potassium content to quite a high figure (4.20 - 4.96 %).

TABLE 5

Injection Experiment

Mean K and Mg content of subtending leaves

Main Nutrient Treatments / Treatment	Complete Long Ashton Nutrient			High K		
	Mg % D.M.	K % D.M.	K/Mg m.e.	Mg % D.M.	K % D.M.	K/Mg m.e.
Mg followed by K	0.639^{K}	4.20^{K}	2.13^{K}	0.677^{K}	4.96^{K}	2.37^{K}
Mg	0.680^{K}	1.84^{K}	0.88^{K}	0.638^{K}	3.27^{K}	1.66^{K}
K	0.371^{M}	3.12^{M}	2.72^{M}	0.413^{M}	4.02^{M}	3.15^{M}
High Mg at Root	0.475	3.31	2.26	0.448	3.07	2.47
Control	0.428	2.05	1.55	0.362	2.46	2.18
L S D 5%	0.098	1.04		0.098	1.04	

superscript K leaves show potassium deficiency

M " " magnesium "

no superscript indicates no deficiency symptoms

In other injection treatments tissues with a wide range of potassium contents (1.84 - 3.27 %) showed potassium deficiency symptoms while plants with quite adequate levels of magnesium (0.371-0.413 %) displayed magnesium deficiency symptoms. In this work the occurrence of symptoms was better described in terms of the K/Mg ratio. A low ratio (e.g. in this case 0.88 or 1.66 respectively) in the tissues gave rise to potassium deficiency and a high ratio (2.72 or 3.15) produced magnesium deficiency symptoms.

To determine more precisely the relationship between these values and symptom expression, the potassium and magnesium content and K/Mg ratio of individual subtending leaves were examined. The data are ranked in order of magnesium percentage (Table 6), potassium percentage (Table 7) and K/Mg ratio (Table 8) and are also represented in the form of histograms in Figure 12.

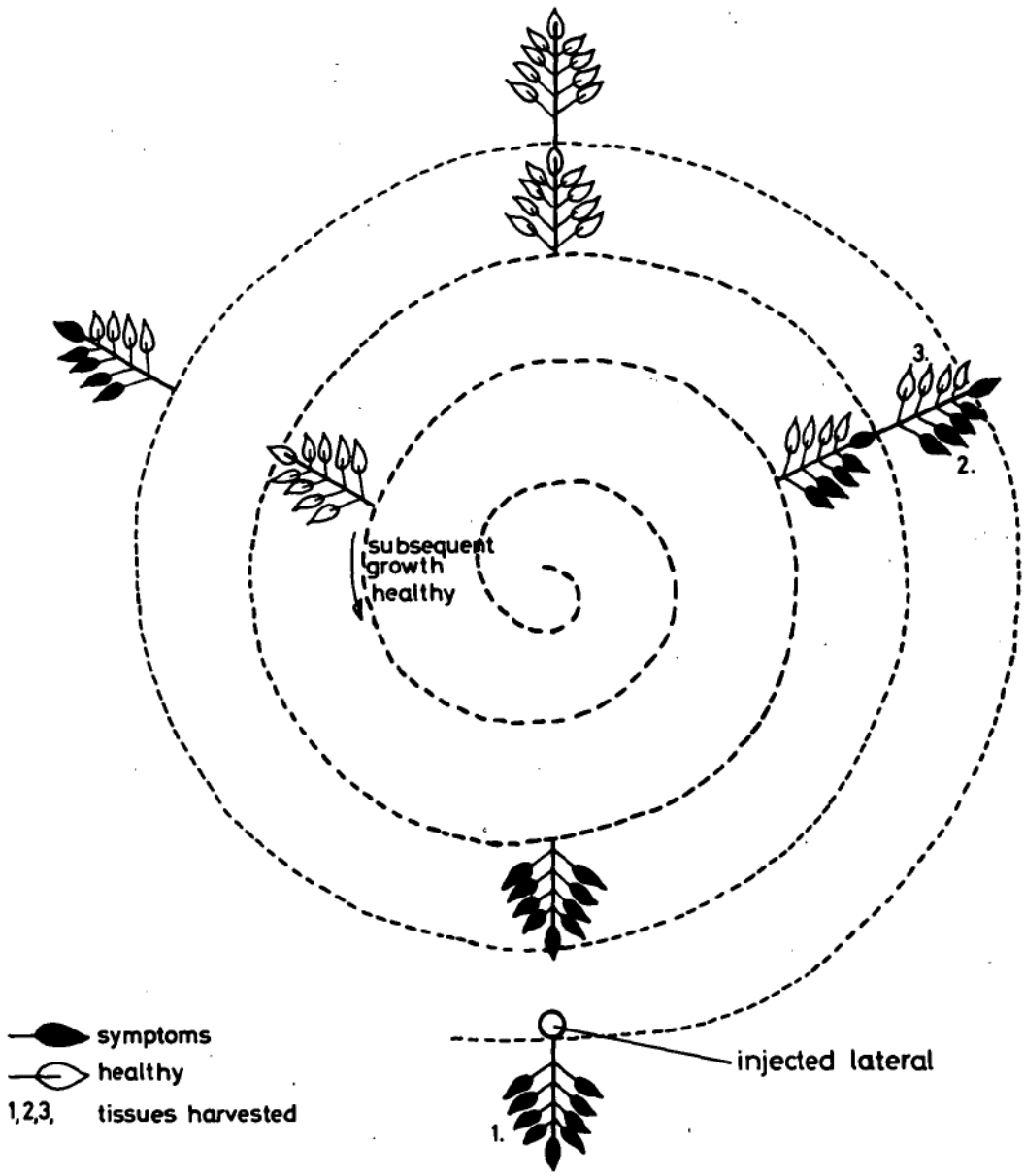
Ranking in order of potassium content did not result in any separation of the tissues into symptom groups. Ranking in order of magnesium content and K/Mg ratio both gave reasonable separation. Indeed, the magnesium levels appeared to play a dominant role in symptom expression. A case could be made, on the basis of the tissues analysed here, for referring to typical potassium deficiency symptoms as magnesium toxicity, since the symptoms are seen at levels above 0.640 % magnesium.

However, examination of a wider range of tissues (Wallace 1925, 1947 and many authors since), and an appreciation of the role of specific K/Mg ratios in optimum plant performance as discussed earlier (page 16), indicate that the better approach may be to use the K/Mg ratio of the tissue to anticipate onset of symptoms. From the data presented here it is apparent that any tomato tissues with a K/Mg ratio above 2.40 are likely to show magnesium deficiency symptoms, while those with ratios below 1.44 are likely to show potassium deficiency symptoms.

FIGURE 11.

Diagramatic representation of the distribution of symptoms resulting from injection at the lateral indicated.

1. subtending leaf harvested for analysis.
2. leaflets showing symptoms harvested for analysis.
3. healthy leaflets harvested for analysis.


subsequent
growth
healthy
3.
2.
1.
injected lateral
symptoms
healthy
1,2,3, tissues harvested

The leaf immediately above the injected lateral showed symptoms only on the side proximal to the injection site (Figure 11). Leaflets were taken for analysis from both sides of this leaf in all plants (Figure 11, sites 2 and 3). Table 9 shows the potassium and magnesium contents of these leaflets expressed as a percentage of the controls. Potassium injection brought about a large increase in the potassium content of the proximal leaflets and their magnesium content was reduced, while on the distal side the magnesium level was relatively unchanged. This indicates that elevated tissue potassium may influence the movement of magnesium from that tissue, tending to influence redistribution of magnesium within the plant and increase the K/Mg ratio of the tissue.

3. Translocation of magnesium by plants under stress of magnesium deficiency.

The object here was to determine if plants could transfer magnesium between their organs, and if this transfer was influenced by potassium and magnesium status.

Tomatoes (var. Grosse Lisse) were grown in nutrient solution as already described. Three groups of plants were established at different potassium and magnesium levels.

1. Complete nutrient solution (solution 1, Table 2).
2. High potassium solution (solution 1 but K increased to 390 ppm).
3. Low magnesium solution (solution 1 but Mg reduced to 4 ppm).

Two plants were established in each container. Eight containers were supplied with each nutrient solution. When the 9th leaf of the tomato plants was just visible microscopically, four containers from each treatment were changed to a solution similar to that in which they were originally grown, except that it contained no magnesium. The other four containers continued in the original solutions. The experiment thus established was a 3 x 2 factorial with four replications.

Table 6

Ion content in relation to symptoms expressed on subtending leaf. Ranked in order of Mg content.

Mg % D.M.	Symptom	K% D.M.	K/Mg m.e.
0.750	K deficiency	1.79	0.771
0.750	"	2.08	0.896
0.750	"	2.78	1.200
0.750	"	3.32	1.433
0.640	NORMAL	1.65	0.827
0.493	"	1.64	1.082
0.493	"	2.68	1.760
0.493	"	2.78	1.825
0.493	"	3.40	2.233
0.461	"	2.17	1.526
0.461	"	2.40	1.686
0.440	"	1.79	1.316
0.440	"	2.40	1.767
0.440	"	3.04	2.237
0.410	"	1.79	1.412
0.410	"	1.79	1.412
0.410	"	2.78	2.193
0.410	"	3.21	2.535
0.410	"	3.50	2.764
0.410	Mg deficiency	3.12	2.463
0.385	NORMAL	1.72	1.445
0.380	Mg deficiency	5.70	4.858
0.365	NORMAL	2.78	1.750
0.365	Mg deficiency	3.60	3.194
0.356	NORMAL	3.04	2.765
0.356	Mg deficiency	3.12	2.838
0.356	Mg deficiency	3.12	2.838
0.353	NORMAL	2.60	2.383

Table 7

Ion content in relation to symptoms expressed on subtending leaf. Ranked in order of K content.

K % D.M.	Symptom	Mg% D.M.	K/Mg m.e.
1.64	NORMAL	0.493	1.082
1.65	"	0.640	0.827
1.72	"	0.385	1.445
1.79	"	0.410	1.412
1.79	"	0.410	1.412
1.79	"	0.440	1.316
1.79	K deficiency	0.750	0.771
2.08	"	0.750	0.896
2.17	NORMAL	0.461	1.526
2.40	"	0.440	1.767
2.40	"	0.461	1.686
2.60	"	0.353	2.383
2.68	"	0.493	1.760
2.78	"	0.365	1.750
2.78	"	0.410	2.193
2.78	"	0.493	1.825
2.78	K deficiency	0.750	1.200
3.04	NORMAL	0.356	2.765
3.04	"	0.440	2.237
3.12	Mg deficiency	0.356	2.838
3.12	"	0.356	2.838
3.12	"	0.410	2.463
3.21	NORMAL	0.410	2.535
3.32	K deficiency	0.750	1.433
3.40	NORMAL	0.493	2.233
3.50	"	0.410	2.764
3.60	Mg deficiency	0.365	3.194
5.70	"	0.380	4.858

Table 8

Ion content in relation to symptoms expressed on subtending leaf. Ranked in order of ratio K : Mg.

K/Mg m.e.	Symptom	Mg% D.M.	K% D.M.
4.858	Mg deficiency	0.380	5.70
3.194	"	0.365	3.60
2.838	"	0.356	3.12
2.838	"	0.356	3.12
2.765	NORMAL	0.356	3.04
2.764	"	0.410	3.50
2.535	"	0.410	3.21
2.463	Mg deficiency	0.410	3.12
2.383	NORMAL	0.353	2.60
2.237	"	0.440	3.04
2.233	"	0.493	3.40
2.193	"	0.410	2.78
1.825	"	0.493	2.78
1.767	"	0.365	2.78
1.760	"	0.440	2.40
1.750	"	0.493	2.68
1.686	"	0.461	2.40
1.526	"	0.461	2.17
1.445	"	0.385	1.72
1.433	K deficiency	0.750	3.32
1.412	NORMAL	0.410	1.79
1.412	"	0.410	1.79
1.316	"	0.440	1.79
1.200	K deficiency	0.750	2.78
1.082	NORMAL	0.493	1.64
0.896	K deficiency	0.750	2.08
0.827	NORMAL	0.640	1.65
0.771	K deficiency	0.750	1.79

TABLE 9

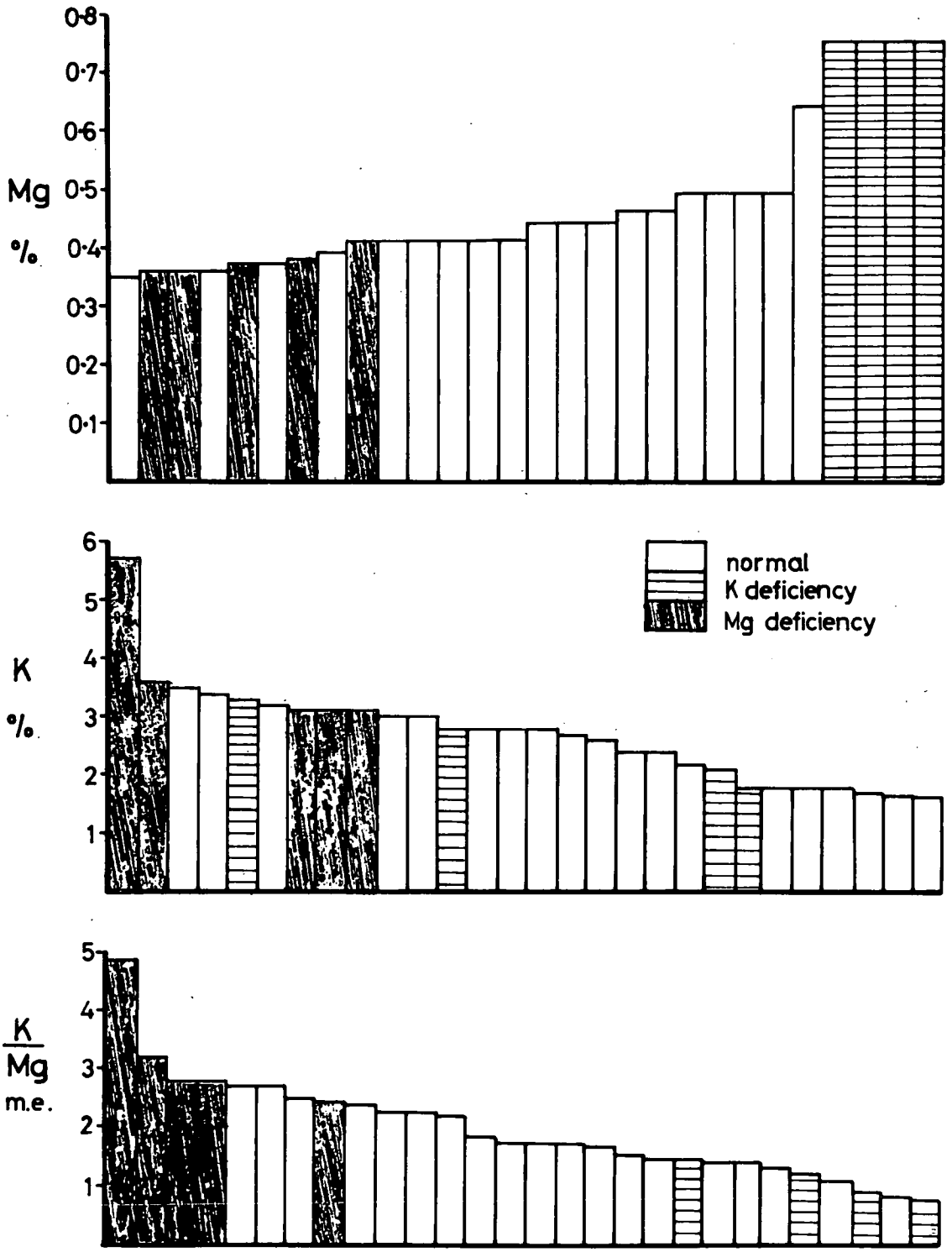
Magnesium content of leaflets taken from opposite sides of the leaf above injection site (expressed as % control)

Treatment	Proximal side		Distal side
	K %	Mg %	Mg %
Control	100.0	100.0	100.0
Normal K, injected K	137.0	85.9	96.9
High K, injected K	186.9	90.0	99.7
L S D 1%	19.4	7.8	N.S.

FIGURE 12.

Histograms showing normal, K deficient and Mg deficient subtending leaves ranked in order of :

above (1) magnesium percentage
middle (2) potassium percentage
below (3) K/Mg ratio


0·8
0·7
0·6
Mg 0·5
% 0·4
0·3
0·2
0·1
6
5
4
K 3
% 2
1
normal
K deficiency
Mg deficiency
5
4
K 3
Mg 2
m.e. 1

At the time of transfer, control plants were healthy, high potassium plants were not as well grown as the controls but were otherwise symptomless, and low magnesium plants showed chlorosis of the older leaves.

Eighteen days after the transfer plants were harvested and divided into the following fractions:

1. Leaves 1 - 6.
2. Stem carrying leaves 1 -6.
3. Leaves 7 - 8.
4. Stem carrying leaves 7 - 8.
5. Leaf 9.
6. New stem.
7. New leaves.

At the time of harvest, the control plants showed slight chlorosis of the lower leaves while those of this group which were transferred to magnesium free solutions were chlorotic to the 7th leaf. High potassium plants which were transferred to magnesium free solution, were severely chlorotic and necrotic to the 9th leaf. The new growth which was expanded after the transfer, had slightly chlorotic leaf tips. Low magnesium plants were chlorotic on leaves 1 - 3 at the time of harvest, but all subsequent growth was normal. The low magnesium plants which were transferred to magnesium free solution, were severely chlorotic to the 9th leaf and all subsequent growth was only slightly chlorotic. Plate 6 shows the appearance of plants, typical of the various treatments, photographed at harvest. Results are summarised in Tables 10 and 11. Both high potassium and low magnesium reduced the percentage and amount of magnesium present in all plant fractions. In the low magnesium treatment, depression of magnesium levels is general throughout the plant. In the case of the high potassium treatment reductions are much greater in the older leaves and in the stem. This suggests that high potassium levels in leaf tissue may help to mobilise magnesium

PLATE 6.

Magnesium deficiency symptoms displayed by tomato plants at the time of harvest of the magnesium transport experiment.

Left to right:

Plant 1. Control. Magnesium deficiency, displayed as intervenal chlorosis, on the basal leaves.

Plant 2. Control, later transferred to solution containing no magnesium. Intervenal chlorosis extends to the 7th leaf. Subsequent growth is healthy.

Plant 3. Normal potassium, low magnesium. Pale growth with mild chlorosis appearing on leaves 1 - 3. Subsequent growth is healthy.

Plant 4. Normal potassium, low magnesium, later transferred to solution containing no magnesium. Severe chlorosis and necrosis is apparent to 9th leaf. Subsequent growth is slightly chlorotic at the leaf tips.

TABLE 10

Magnesium transport Experiment

Magnesium content of tomato plant fractions

Treatment	Leaves 1-6		Lower Stem		Leaves 7-8		Upper Stem		Marked leaf		New Stem		New leaves	
	%	mg	%	mg	%	mg	%	mg	%	mg	%	mg	%	mg
Complete														
1. Whole period	0.562	6.41	0.320	2.09	0.332	4.55	0.105	1.40	0.292	0.47	0.204	0.11	0.298	0.89
2. Change-leaf 9	0.288	2.66	0.133	0.83	0.070	0.87	0.072	0.41	0.82	0.12	0.067	0.03	0.142	0.22
High K														
1. Whole period	0.452	4.25	0.273	1.80	0.291	3.78	0.202	1.32	0.306	0.41	0.171	0.12	0.336	0.81
2. Change-leaf 9	0.190	1.73	0.110	0.67	0.054	0.56	0.076	0.35	0.72	0.06	0.092	0.02	0.113	0.14
Low Mg														
1. Whole period	0.195	2.12	0.141	1.01	0.137	1.57	0.101	0.61	0.126	0.19	0.097	0.05	0.183	0.33
2. Change-leaf 9	0.105	0.76	0.086	0.40	0.064	0.52	0.141	0.24	0.073	0.19	0.090	0.02	0.131	0.11
L S D 1%	0.079	0.98	0.051	0.47	0.048	0.72	0.045	0.54	0.041	0.29	0.058	0.03	0.32	0.18

TABLE 11

Magnesium transfer experiment

Characteristics of new leaves expanded after transfer to magnesium free conditions.

	Nutrient status		
	Normal	High K	Low Mg
Mg content (%)			
Normal growth	0.289	0.336	0.183
Minus Mg growth	0.142	0.113	0.131
Leaf weight (g)			
Normal growth	2.96	2.41	1.87
Minus Mg growth	1.65	1.19	0.83
Amount Mg (mg)			
Normal growth	0.892	0.814	0.329
Minus Mg growth	0.219	0.135	0.107

in its re-allocation to other plant organs as was inferred earlier (p. 70) from the results of the plant injection work.

Reduction in plant magnesium levels following transfer to magnesium free solutions (Table 10) is greater in leaves 7 - 8 than in leaves 1 - 6.

Leaves 7 - 8 were expanding rapidly during the 18 days following transfer, and this is reflected in their lower magnesium levels. Leaves 1 - 6 however, were fully expanded, or more nearly so, and their lower magnesium contents were more likely due to re-allocation of magnesium taken up prior to the change-over.

Table 11 shows that magnesium is transferred to new growth under magnesium free conditions. In no case however does the level of magnesium in parts elaborated after the transfer reach the level in the comparable parts of control plants with continued access to nutrient solution.magnesium. In addition, in all treatments, the amount of new growth produced under magnesium free conditions was less.

Plants which were grown in normal nutrient solution before the transfer to magnesium free medium, translocated most magnesium (0.219 mg) to the new leaves and also produced the greatest amount of new growth (1.65 g) with the highest magnesium content (0.142 %). High potassium plants had more magnesium in the new growth (0.135 mg), than did low magnesium plants (0.107 mg). This is a reflection of the greater amount of magnesium present in the basal leaves of the high potassium plants (4.25 mg) than was present in the equivalent leaves of the plants grown in the low magnesium solution (2.12 mg).

TABLE 12

Distribution experiment

Nutrient solutions

Element	Soln. 1 ppm	Soln. 2 ppm	Soln. 3 ppm	Soln. 4 ppm	Soln. 5 ppm
K	195	390	390	195	39
Mg	24	24	4	48	48
Ca	200	200	200	200	200
N	210	210	210	210	210
P	41	41	41	41	41
Fe	5.6	5.6	5.6	5.6	5.6
Mn	0.55	0.55	0.55	0.55	0.55
Cu	0.064	0.064	0.064	0.064	0.064
Zn	0.065	0.065	0.065	0.065	0.065
B	0.37	0.37	0.37	0.37	0.37
Mo	0.019	0.019	0.019	0.019	0.019
Co	0.006	0.006	0.006	0.006	0.006
Cl	3.55	3.55	3.55	3.55	3.55

Solution 1. Control, Long Ashton Solution

2. High K, normal Mg

3. High K, low Mg

4. Normal K, high Mg

5. Low K, high Mg

4. Effect of different levels of potassium and magnesium on the distribution of these and other ions within the plant.

A sand culture experiment was set up with five combinations of three levels of potassium and magnesium supplied in solutions as set out in Table 12. It was not possible to examine all nine combinations, and five were chosen to give a range of combinations around the normal levels represented by those of the Long Ashton nutrient solution (Hewitt 1963). In the light of previous results that potassium reduced uptake of magnesium by barley roots, together with the effect that injecting tissues with potassium had on the magnesium levels of the tissues, main emphasis was placed on the effect of high levels of potassium on the amount and distribution of potassium and magnesium. Because the experiment involved dissection of plants into parts which were often very small (e.g. immature leaves and inflorescences) it was felt that high levels of replication (in this case 10) should be used for a restricted number of treatments, so that reliability of small differences could be established, and in some cases, so that material could be bulked to obtain a sufficiently large sample for chemical analysis.

The experiment was laid out in two 5 x 5 latin squares. Each container was planted with 24 barley seeds (var. Bolivia) which were later thinned to give 12 evenly spaced plants. Two plants were harvested from each container at 28, 42, 56, 70, 91 and 121 days after planting. The plants were divided into roots, leaves, main stem and individual tillers. Up to 18 tillers were produced by advanced plants. The main stem and first tiller were further divided into basal leaves, node leaves, flag, stem and inflorescence. All plant parts were dried, weighed, ground and analysed chemically as described earlier (page 53).

TABLE 13

Distribution experiment

Dry matter yields (g)

Treatment	Plant parts	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	0.041	0.207	0.348	0.799	1.858	3.870
	Tillers	-	0.024	0.193	1.213	2.504	7.225
	Roots	0.050	0.232	0.530	2.025	4.350	10.782
	TOTAL	0.091	0.463	1.081	4.037	8.712	21.877
HIGH K	M.S. & T_1	0.031	0.105	0.247	0.709	1.984	3.566
NORMAL Mg	Tillers	-	0.003	0.051	0.368	2.417	5.824
	Roots	0.049	0.100	0.275	1.011	4.290	7.227
	TOTAL	0.080	0.208	0.473	2.088	8.691	16.617
HIGH Mg	M.S. & T_1	0.031	0.109	0.273	0.603	1.846	3.165
NORMAL K	Tillers	-	0.003	0.058	0.323	1.902	5.510
	Roots	0.050	0.099	0.325	0.925	3.690	9.132
	TOTAL	0.081	0.211	0.656	1.851	7.438	18.707
L S D 1%	Totals	0.009	0.051	0.178	0.211	0.416	0.785
	Parts	0.006	0.042	0.143	0.199	0.389	0.780

TABLE 14

Distribution experiment

Amount (mg) of potassium in plant parts

Treatment	Plant parts	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	2.799	7.014	19.923	26.024	18.843	47.895
	Tillers	-	0.398	9.417	41.337	25.704	103.490
	Roots	0.770	2.857	2.806	8.606	19.371	38.430
	TOTAL	3.569	10.269	34.146	75.967	63.918	189.815
HIGH K NORMAL Mg	M.S. & T_1	1.737	3.738	7.584	21.816	53.989	53.099
	Tillers	-	0.127	1.445	13.760	53.838	102.606
	Roots	0.277	0.940	2.850	7.018	12.246	22.566
	TOTAL	2.014	3.805	11.879	42.594	120.073	178.271
HIGH Mg NORMAL K	M.S. & T_1	1.519	3.879	9.155	16.799	34.648	33.975
	Tillers	-	0.103	1.928	13.320	49.288	84.890
	Roots	0.327	0.570	2.486	4.622	15.062	15.520
	TOTAL	1.846	4.552	13.569	34.741	98.998	134.385
L S D 1%	Totals	0.146	0.230	1.500	10.114	12.222	14.866
	Parts	0.121	0.197	1.107	3.101	5.183	7.404

TABLE 15

Distribution experiment

Amount (mg) of magnesium in plant parts

Treatment	Plant part	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	0.113	0.416	1.007	2.073	3.037	4.300
	Tillers	-	0.044	0.378	2.947	3.507	8.735
	Roots	0.067	0.127	0.179	0.689	1.202	7.023
	TOTAL	0.180	0.587	1.564	5.746	7.746	20.058
HIGH K NORMAL Mg	M.S. & T_1	0.164	0.292	0.571	1.789	2.299	3.587
	Tillers	-	0.008	0.108	0.769	3.024	5.558
	Roots	0.035	0.046	0.112	0.382	1.258	4.264
	TOTAL	0.199	0.346	0.791	2.940	6.581	13.409
HIGH Mg NORMAL K	M.S. & T_1	0.090	0.342	1.068	2.216	3.234	4.868
	Tillers	-	0.007	0.165	1.109	4.459	8.904
	Roots	0.050	0.052	0.194	0.398	1.382	4.328
	TOTAL	0.140	0.401	1.427	3.723	9.075	18.100
L S D 1%	Totals	0.060	0.141	0.210	0.560	1.101	2.449
	Parts	0.030	0.043	0.209	0.210	0.986	0.997

Only the control (solution 1), high K - normal Mg (solution 2) and high Mg - normal K (solution 4) treatments will be discussed. Both high potassium and high magnesium reduced the dry matter yield of barley plants (Table 13), the effect being noticed in the early harvests and continuing throughout the experiment. The amount of potassium and magnesium in the plant fractions throughout the experiment is shown in Tables 14 and 15. A depression in the amount of potassium taken up was established in the high potassium treatment by the 28th day, before any difference in yield of dry matter was apparent, and continued throughout most of the experiment (Table 14). At the same time, plants of the high potassium treatment showed a depression in magnesium level after 28 days compared with the control, and this effect persisted to the end of the experiment (Table 15). In general, the amount of root magnesium was reduced along with that in other plant parts (Table 15). However, in the early harvest (28 days) the amount of magnesium contained in the roots was unchanged. When root magnesium content was expressed as a percentage of total plant magnesium (Table 21), a slight reduction was recorded early in the growing period. Rate of root magnesium accumulation may bear some relation to the rate of root growth (Figure 19).

The high magnesium treatment depressed the amount of potassium taken up by the plants but had little effect on the amount of magnesium taken up, when compared with the control.

High potassium almost invariably increased the percentage potassium content in plant parts, when compared with the control. For example, the percentage potassium content of the leaf attached to the first node of the main stem rose from 3.20 % in the control plants to 4.82 % in high potassium plants (Table 16). In contrast, the potassium

TABLE 16

Percent content of K and Mg in plant parts (at 121 day harvest)

Plant part	Potassium (%)		Magnesium (%)	
	Control	High K	Control	High K
MAIN STEM				
Inflor.	2.03	2.08	0.173	0.175
Leaves N_1	3.20	4.82	0.568	0.448
N_2	2.40	4.26	0.499	0.408
N_3	2.54	3.32	0.368	0.324
N_4	2.64	3.32	0.319	0.239
N_5	2.24	3.32	0.318	0.283
Flag	3.24	3.80	0.253	0.212
Stem	3.87	4.32	0.060	0.055
TILLER 1.				
Inflor.	1.76	1.61	0.186	0.203
Leaves N_1	2.95	4.05	0.534	0.498
N_2	2.54	3.86	0.462	0.376
N_3	2.49	3.51	0.385	0.296
N_4	2.82	3.57	0.375	0.298
N_5	2.07	3.65	0.325	0.230
Flag	3.10	3.50	0.348	0.192
Stem	3.08	4.17	0.064	0.057

TABLE 17

Content (%) of K, Mg and Na in plant tillers (at 121 day harvest)

Tiller No.	K		Mg		Na	
	Control	High K	Control	High K	Control	High K
1	2.33	2.85	0.226	0.206	0.63	0.27
2	2.87	3.60	0.265	0.181	0.84	0.31
3	2.78	3.51	0.232	0.204	0.74	0.28
4	2.82	3.36	0.275	0.199	0.58	0.25
5	2.68	3.31	0.239	0.204	0.68	0.28
6	2.68	3.61	0.221	0.196	0.49	0.25
7	2.68	3.80	0.213	0.214	0.51	0.21
8	2.99	3.44	0.218	0.178	0.60	0.31
9	2.81	4.15	0.279	0.171	0.85	0.28
10	2.82	3.90	0.226	0.168	0.49	0.31
11	3.36	4.00	0.204	0.162	0.79	0.25
12	4.00	4.93	0.196	0.177	0.55	0.50
13	3.85	5.00	0.202	0.215	0.55	
14	3.76		0.170		0.99	
15	3.66		0.166		0.59	
16	3.50		0.202		0.42	
17	2.78		0.126		0.19	
18	3.33		0.213		0.67	

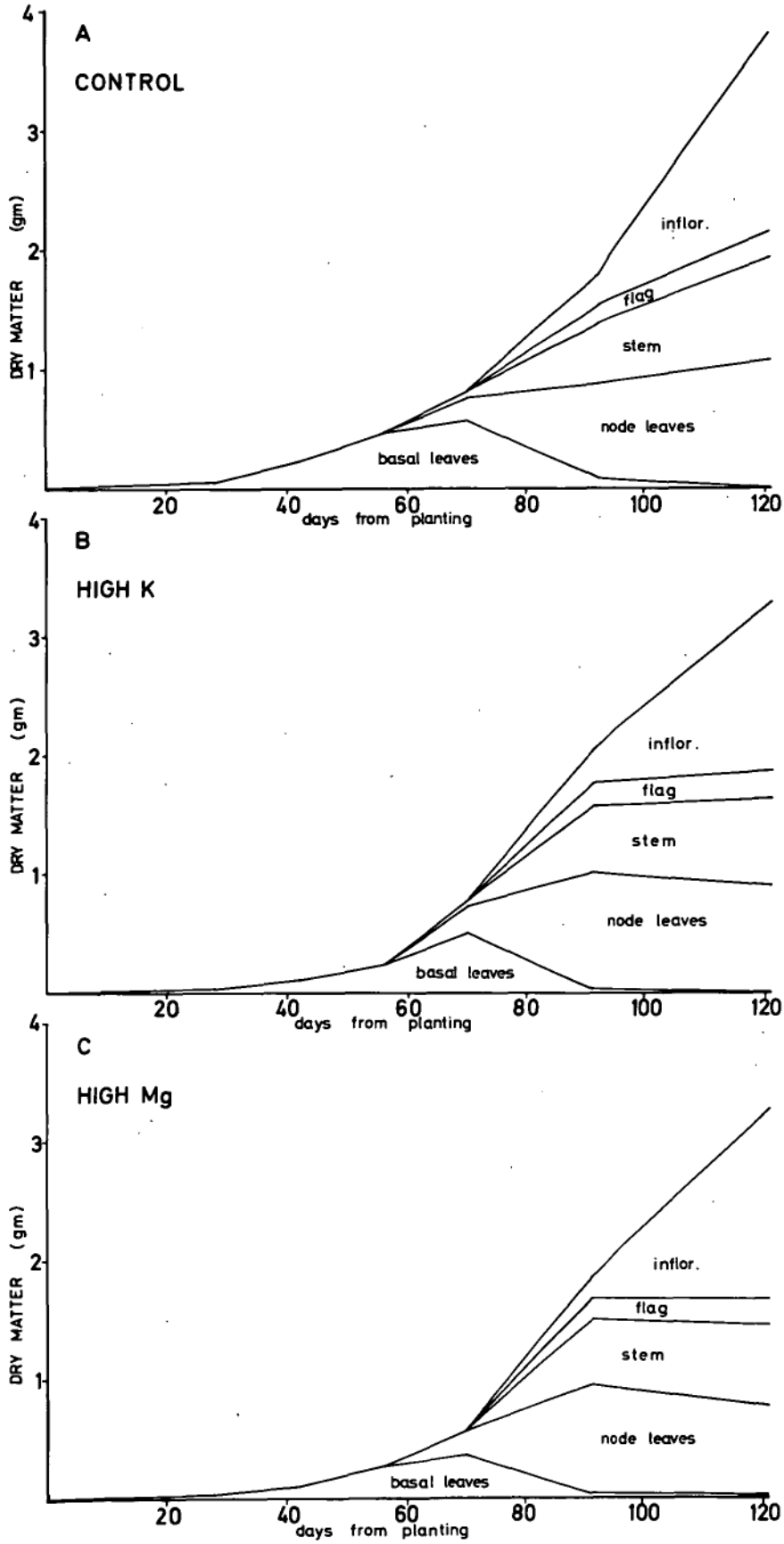
content of the inflorescence which was developing rapidly at 121 days was constant, 2.03 % in controls compared with 2.08 % in high potassium plants. Elevated potassium levels were associated with reduced magnesium levels in all vegetative parts of the plant. Again, taking the leaf on the first node of the main stem as an example, its magnesium content was reduced from 0.568 % in controls to 0.448 % in the high potassium treatment (Table 16). The relationship did not hold for the inflorescence, whose magnesium level seemed stable (0.173 % compared with 0.175 %) irrespective of treatment. This stability of magnesium content in plant reproductive parts, irrespective of the magnesium status of the rest of the plant, has been used as evidence of plant magnesium mobility (Fudge 1939; Dix and Bishoff 1930).

In both the high potassium treatment and the control there is the same level of magnesium present in the nutrient solutions (Table 12). This level of magnesium (24 ppm) is that present in the Long Ashton solution which normally supports healthy plant growth (Hewitt 1966). High potassium in the nutrient medium, however, reduced the magnesium level in all tillers when compared to the controls (Table 17), in many cases to a level below that said to be critical for the onset of hypomagnesaemia (0.2 %, Wolton 1963). In some tillers the magnesium level was as low as 0.162 % and in no tiller was it above 0.215 %. The high potassium treatment also reduced the number of tillers from 18 to 13. The percentage magnesium also fell as parts further up the main stem were examined (Table 16). At the extremes, the magnesium percentage in the flag (0.212 %) was approximately half that of the leaf at the first node (0.448 %). A similar relationship was found for the first tiller, 0.192 % and 0.376 % respectively.

FIGURE 13.

Changes in distribution of dry matter in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. control - Long Ashton Solution
B. high K - 390 ppm
C. high Mg - 48 ppm


A
CONTROL
DRY MATTER (gm)
inflor.
flag
stem
node leaves
basal leaves
days from planting
B
HIGH K
DRY MATTER (gm)
inflor.
flag
stem
node leaves
basal leaves
days from planting
C
HIGH Mg
DRY MATTER (gm)
inflor.
flag
stem
node leaves
basal leaves
days from planting

The data for the main stem and first tiller were graphed in the manner usual for this type of study (Williams 1955; Cizek 1960). The dry weight or the amount of a particular element was plotted against the time of harvest (e.g. Figure 13). Data for the main stem and first tiller were combined for the purposes of presentation. The value of each component was plotted, one above the other, in a summation curve. In this way, the value relating to any component is represented by the vertical distance between the two lines demarcating the area of the graph relating to that component. The uppermost line represents the sum of all components and therefore the total amount of a particular substance in the main stem and first tiller. Information on dry matter production, potassium, magnesium, calcium, sodium and phosphorus contents, as affected by the level of potassium and magnesium in the medium for each time of harvest, are presented in this from in Figures 13 - 18.

Dry Matter Production: Dry matter production by the main stem and first tiller is shown in Figure 13. Both the high potassium treatment (Figure 13 b) and the high magnesium treatment (Figure 13 c) reduced total dry matter production by about the same amount. The high magnesium treatment reduced basal leaf production more than did the high potassium treatment. Other than this the pattern of development of the plant parts was remarkably similar for the three treatments. More node leaf dry matter was produced by both treatments at 91 days than by the control. This was reduced in both cases at 121 days, more noticeably in the case of the high magnesium treatment. In the control plants dry matter production of node leaves increased gradually throughout the growing period.

FIGURE 14.

Changes in distribution of potassium in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. control - Long Ashton Solution
B. high K - 390 ppm
C. high Mg - 48 ppm

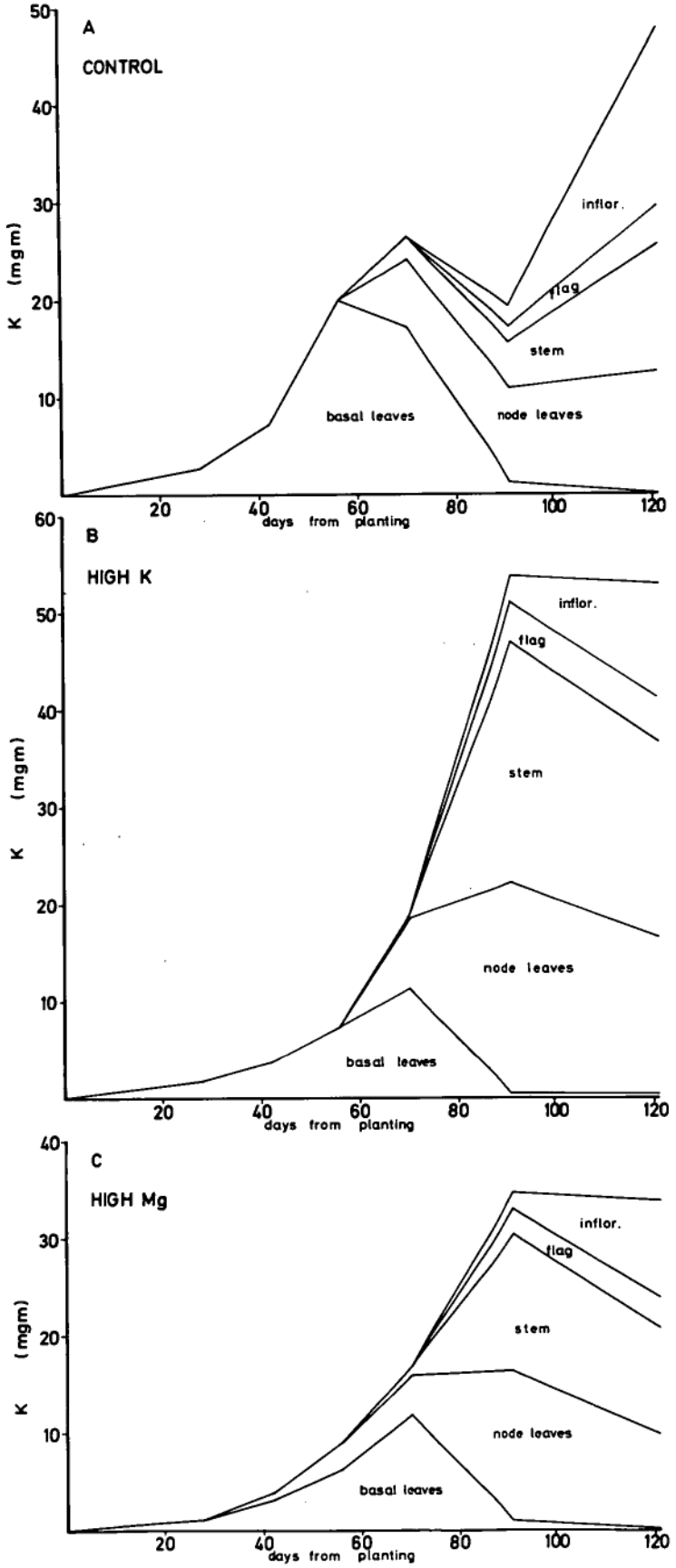
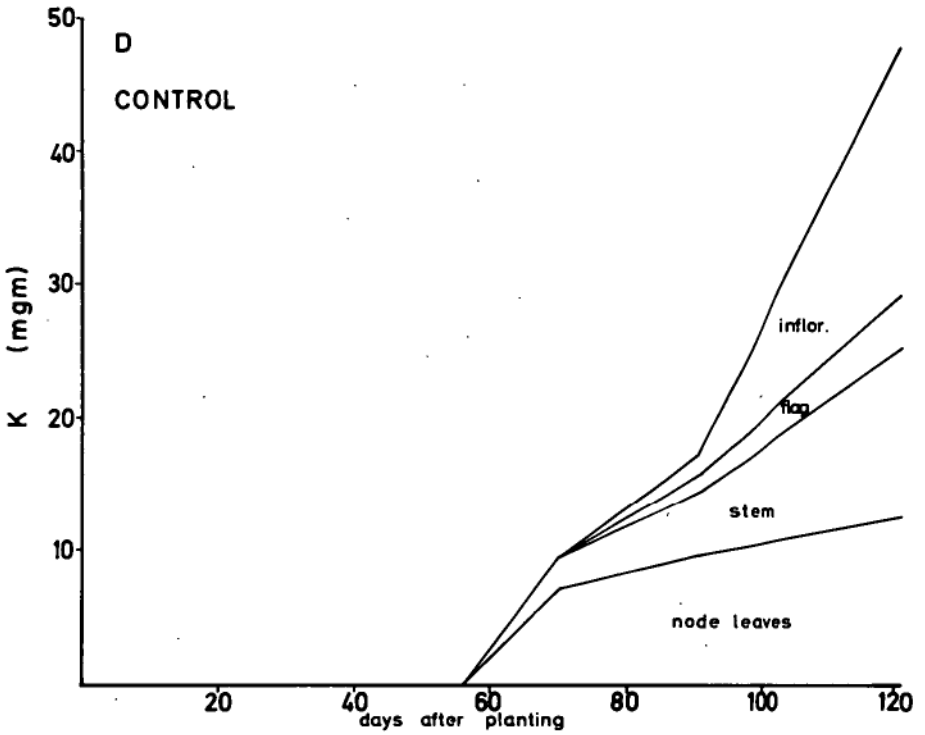

A
CONTROL
K (mgm)
inflor.
flag
stem
basal leaves
node leaves
days from planting
B
HIGH K
K (mgm)
inflor.
flag
stem
node leaves
basal leaves
days from planting
C
HIGH Mg
K (mgm)
inflor.
flag
stem
node leaves
basal leaves
days from planting

FIGURE 14D.

Changes in distribution of potassium in the main stem and first tiller of barley plants during the growth period of 121 days, neglecting the content of the basal leaves.


D
CONTROL
50
40
30
20
10
K (mgm)
inflor.
flag
stem
node leaves
20
40
60
80
100
120
days after planting

Potassium : Changes in potassium distribution during development displayed an interesting pattern. In the plants of the control treatment there was a large accumulation of potassium in the basal leaves (Figure 14 a) which did not occur in the high potassium or high magnesium plants (Figure 14b and c). The accumulation was greater than would be expected from the greater dry matter production of this component. The basal leaves had a higher potassium content (5.53 % at 70 days compared with 3.60 % and 2.65 % respectively for the other treatments). Because of this higher potassium content, when basal leaves were lost, as occurred in all treatments (Figure 13), there was a consequent greater loss of potassium from the control plants. Growth of other components of the control plants and accumulation of potassium by them could not compensate for this loss of potassium which was reflected in a drop in the overall potassium content at 91 days. This is in startling contrast with total potassium content in the case of the other two treatments where loss of basal leaf potassium was compensated for by development of other components, so that no drop in total potassium resulted. That the drop in total potassium was associated with the loss of basal leaves by the control plants can be seen clearly in Figure 14 D. which shows the accumulation of potassium when the basal leaf component was excluded.

All components, in all treatments, other than the basal leaves, steadily accumulated potassium throughout the experimental period until the 91 day harvest. To this stage much more potassium was accumulated by the high potassium plants (5.399 mg) than was accumulated by high magnesium (3.465 mg) or control plants (1.884 mg). This greater

absorption of potassium in the high potassium treatment was accounted for in a different manner to the absorption of potassium in the control treatment. In the high potassium treatment, the greatest accumulation of potassium was in the node leaves and stem while greatest accumulation occurred in the basal leaves in the case of control plants. In the high potassium treatment many leaves became prematurely senescent and abscissed from the plant early. This, however, does not explain the difference between the distribution of potassium in the basal leaf section of control and high potassium treatments because their percentage potassium content also differed greatly being 5.53% and 3.60 % respectively.

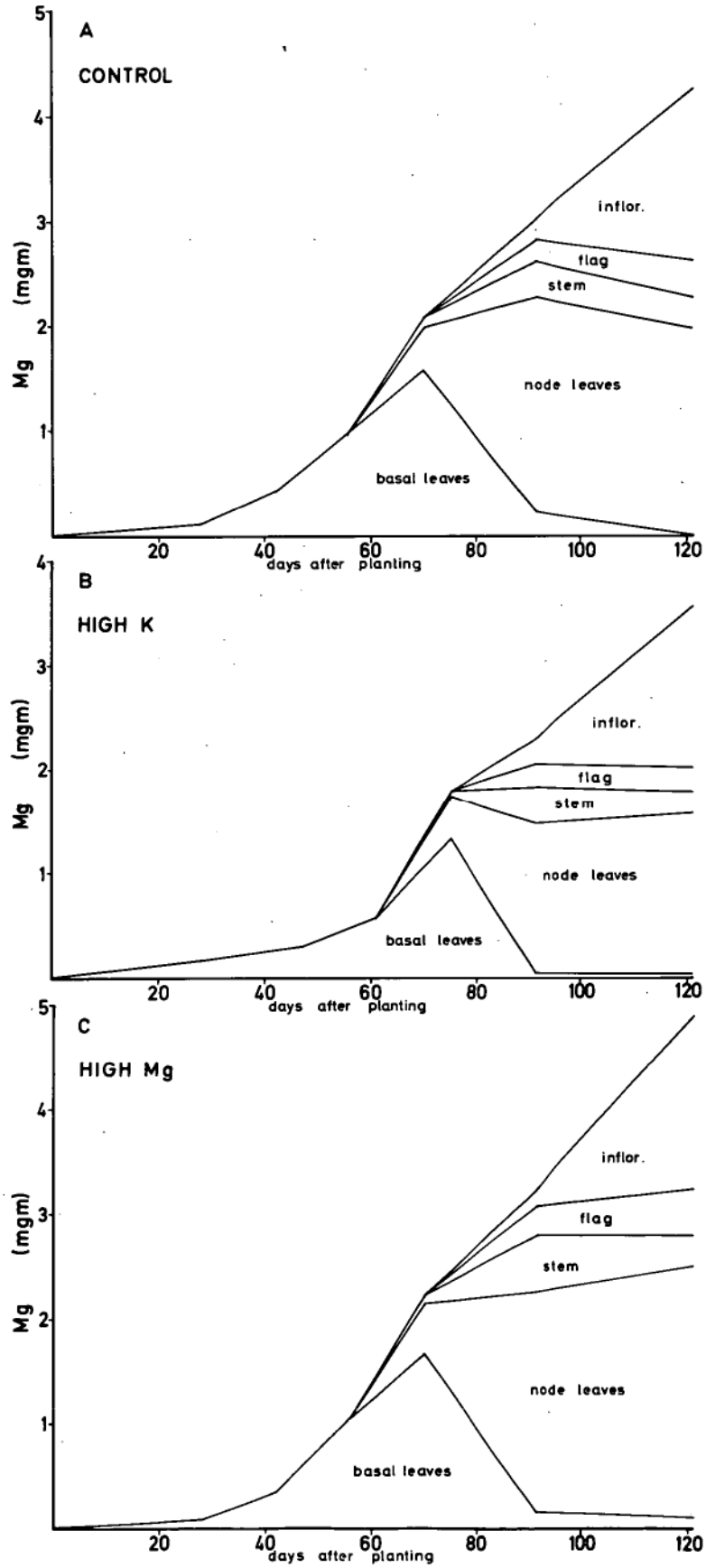
Plant parts of both the high potassium and high magnesium treatments reached their maximum potassium content at 91 days (Figure 14 b & c). Total potassium absorbed was greater in the high potassium treatment (53.99 mg) than in the high magnesium treatment (34.65 mg, Table 14). The latter was lower than the amount of potassium finally accumulated by the control treatment (47.90 mg). In the case of high potassium and high magnesium treatments, where total potassium did not increase after 91 days, the increase in inflorescence potassium, as the reproductive organs developed, was accounted for by a decrease in the potassium of other components, namely stems and node leaves (Figure 14 b & c).

Magnesium: Changes in the magnesium content are illustrated in Figure 15. The percentage magnesium content of the basal leaf varied very little and all changes in the amount of magnesium present were in accord with changes in dry matter production. Less magnesium was accumulated in the node leaves, stem and flag when potassium was high than was the case with the control. In neither case was there any decrease in the node leaf or flag magnesium as the inflores-

FIGURE 15.

Changes in the distribution of magnesium in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. control - Long Ashton Solution
B. high K - 390 ppm
C. high Mg - 48 ppm


A
CONTROL
inflor.
flag
stem
node leaves
basal leaves
Mg (mgm)
days after planting
B
HIGH K
inflor.
flag
stem
node leaves
basal leaves
Mg (mgm)
days after planting
C
HIGH Mg
inflor.
flag
stem
node leaves
basal leaves
Mg (mgm)
days after planting

cence developed. Floral magnesium must, therefore, come from continued root uptake of by re-allocation from later tillers. There is some indication (Figure 15 b & c) that at high levels of potassium and of magnesium, stem magnesium may be drawn on as the inflorescence develops, but this trend was only slight and stem magnesium was only a small part of the magnesium involved. On the whole, there was no radical effect of high potassium levels on the distribution of magnesium within the main stem and first tiller.

Calcium: Plant calcium was reduced by increasing the potassium level in the nutrient solution (Drake and Scarseth 1940; Evans, Lathwell and Menderski 1950; Laughlin and Restad 1964; Resnik 1964). Magnesium also has been shown to reduce the calcium content of plants (Smith et al.1954). Because of the importance of calcium in plant metabolism (Epstein 1965) and, in particular, because of the relation between plant magnesium and calcium (Gauch 1940), the effect of elevated levels of potassium and magnesium on the distribution of calcium within the plant parts was studied in this experiment.

High potassium in the medium greatly reduced the uptake of calcium by plants a t all stages (Table 18). Reduced calcium content occurred in all plant parts. At the time of final harvest, root calcium, although still less than that found in the control plants, greatly increased over the level present in previous harvests (Table 18). This was associated with greater root dry matter, without any marked change in percentage calcium content.

Figure 16 shows that the greatest reduction in plant calcium took place in the basal leaves. High potassium

and high magnesium were associated with reductions of about equal magnitude compared to the control. Node leaf calcium increased gradually throughout the period of the experiment in the high potassium plants. There was a similar trend in the node leaf calcium of the high magnesium treatment although some depression was recorded at 91 days.

The inflorescence of high potassium plants contained as much calcium as did the inflorescence of control plants. On the other hand, the inflorescence of high magnesium plants contained less calcium. As mentioned previously inflorescence potassium levels remained unchanged over a wide range of total plant potassium levels and the high potassium treatment had no influence on the amount of potassium in the inflorescence (Figure 14b). There was consequently no antagonism between potassium and calcium to reduce the inflorescence calcium level. In the case of high magnesium plants, however, the inflorescence magnesium was increased (Figure 15 c), and antagonism between magnesium and calcium may have contributed to the decrease in calcium content.

Sodium: The ability of plants to distinguish between chemically similar ions such as potassium and sodium has been the subject of much speculation (McClurkin and McClurkin 1967). The interaction between potassium and sodium at uptake is well known and has been investigated frequently (Overstreet et al. 1952; Epstein and Hagen 1952; Fried and Noggle 1958; Bange 1959). Although it has been shown in some plants that sodium can partially substitute for potassium (Hewitt 1963; Lehr 1951), it is only in microorganisms (Allen and Arnon 1955) and a restricted group of plants such as Atriplex L. (Chenopodiacae) that sodium has been shown to be an essential plant micro-nutrient (Brownell and Wood 1957). It is surprising that it has not been shown to be essential for many more plants because of its demonstrated role as an enzyme activator,

TABLE 18

Distribution experiment

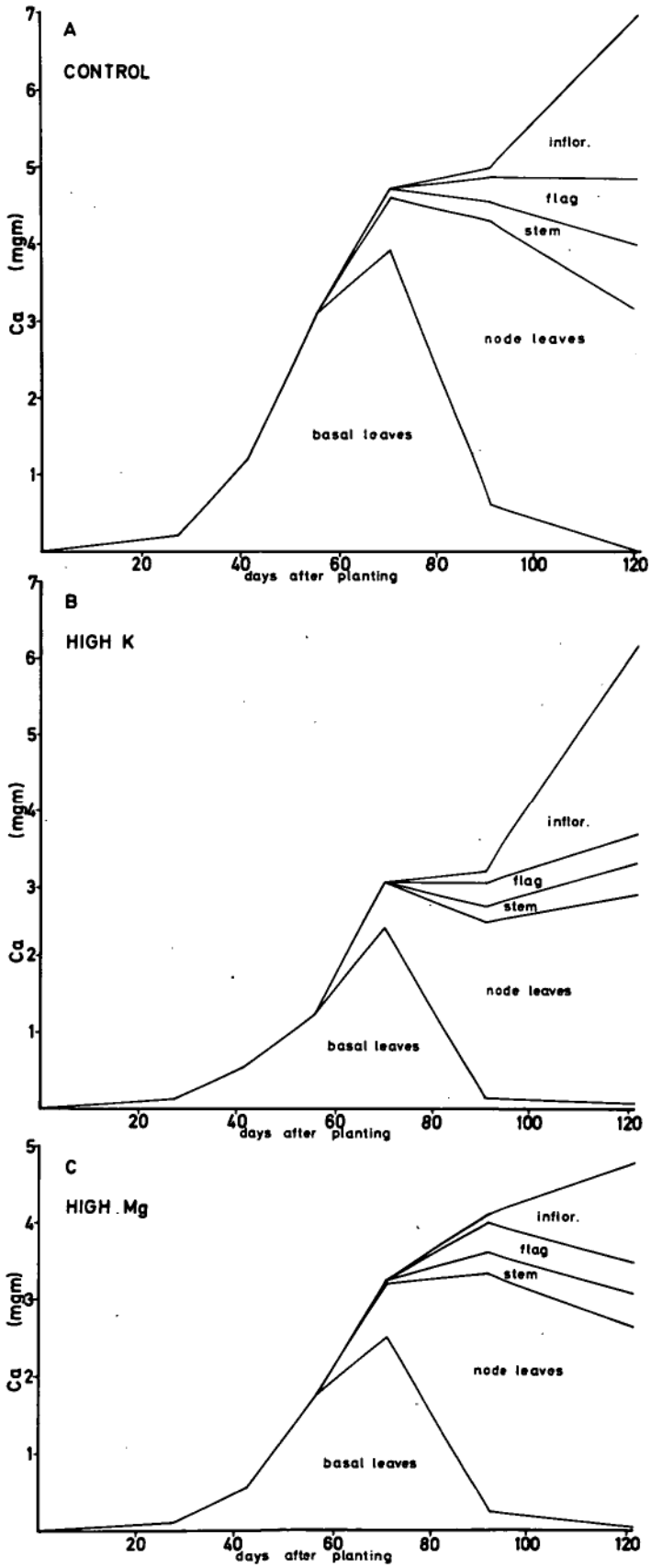
Amount (mg) of calcium in plant parts

Treatment	Plant part	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	0.215	1.220	3.112	4.711	5.012	7.075
	Tillers	-	0.079	0.496	2.675	5.682	18.317
	Roots	0.100	0.476	0.606	0.464	11.372	94.438
	TOTAL	0.315	1.775	4.214	7.850	22.066	119.830
HIGH K NORMAL Mg	M.S. & T_1	0.129	0.518	1.523	2.978	3.229	6.086
	Tillers	-	0.008	0.108	1.326	3.838	10.624
	Roots	0.020	0.090	0.123	0.709	3.511	69.335
	TOTAL	0.149	0.616	1.754	5.013	10.578	86.045
L S D 1% Total		0.161	0.943	1.844	1.880	2.487	8.441
Parts		0.101	0.447	1.119	1.386	1.982	3.229

FIGURE 16.

Changes in the distribution of calcium in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. - control - Long Ashton Solution
B. - high K - 390 ppm
C. - high Mg - 48 ppm


A
CONTROL
inflor.
flag
stem
node leaves
basal leaves
Ca (mgm)
days after planting
B
HIGH K
inflor.
flag
stem
node leaves
basal leaves
Ca (mgm)
days after planting
C
HIGH Mg
inflor.
flag
stem
node leaves
basal leaves
Ca (mgm)
days after planting

particularly of enzymes associated with ion uptake (Gruener and Neuman 1966; McClurkin and McClurkin 1967). Because of this well established association of potassium and sodium, the effect of the treatments applied in this experiment on sodium uptake and distribution were examined.

Total sodium uptake by the plants was greatly reduced by high potassium in the medium. Reduction took place in all plant parts (Table 19). Detailed examination (Figure 17) of the main stem and first tiller showed that high potassium greatly reduced the sodium content of all fractions although inflorescence sodium was reduced least of all. This may be associated with the lack of effect of high potassium levels in the nutrient medium on the potassium level of the inflorescence, mentioned previously. With the obvious exception of the basal leaves, the sodium content of all fractions increased gradually throughout the growing period. In the presence of high magnesium, the sodium content of the node leaves initially increased but dropped after the 91 day harvest while the sodium content of the stem continued to increase. Flag sodium decreased in both treatments compared to the control.

Phosphorus: Tissue magnesium levels have been correlated with those of phosphorus by several workers (Miller 1938; Zimmerman 1947; Truog *et al*. 1947; Mulder 1953). This correlation is probably due to the involvement of magnesium in the activation of many enzymes involving phosphate and to the function of magnesium in stabilizing ATP (Lehninger 1965). Therefore, it was felt that the changes in plant phosphorus which occurred in the present experiment should be recorded.

High potassium had no effect on the total uptake of phosphorus. Towards the end of the experimental period, more phosphorus accumulated in the roots of the high potassium plants than in the roots of the control plants (Table 20).

TABLE 19

Distribution experiment

Amount (mg) of sodium in plant parts

Treatment	Plant parts	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	0.224	1.384	1.927	4.162	6.411	12.048
	Tillers	-	0.105	0.809	4.707	7.746	24.659
	Roots	0.197	0.510	0.260	0.412	2.748	12.224
	TOTAL	0.421	1.999	2.996	9.281	16.905	48.931
HIGH K NORMAL Mg	M.S. & T_1	0.215	0.628	0.772	1.154	2.889	6.090
	Tillers	-	-	0.351	0.514	4.154	7.841
	Roots	0.151	0.095	0.260	0.636	2.449	7.629
	TOTAL	0.366	0.723	1.383	2.304	9.492	21.560
L S D 1%	Totals	0.060	1.107	1.244	4.229	6.429	10.531
	Parts	0.053	0.401	0.468	0.982	1.136	2.810

TABLE 20

Distribution experiment

Amount (mg) of phosphorus in plant parts

Treatment	Plant parts	Harvest (days)					
		28	42	56	70	91	121
CONTROL	M.S. & T_1	0.281	1.029	1.748	2.811	4.128	7.079
	Tillers	-	0.152	1.013	5.526	6.001	15.674
	Roots	0.085	0.273	0.597	1.807	6.403	16.703
	TOTAL	0.366	1.454	3.358	10.144	16.532	39.457
HIGH K NORMAL Mg	M.S. & T_1	0.190	1.494	1.565	2.974	5.037	6.941
	Tillers	-	0.023	0.336	5.008	4.739	12.704
	Roots	0.055	0.118	0.326	1.526	4.368	24.198
	TOTAL	0.245	1.635	2.227	9.508	17.142	43.843
HIGH Mg NORMAL K	M.S. & T_1	0.200	0.610	1.533	4.037	3.989	5.516
	Tillers	-	0.025	0.388	2.015	7.133	13.300
	Roots	0.065	0.111	0.386	1.298	5.822	13.048
	TOTAL	0.265	0.746	2.307	7.350	16.944	31.864
L S D 1%	Totals	0.101	0.346	0.988	1.446	1.889	2.989
	Parts	0.100	0.328	0.564	1.186	1.642	2.444

FIGURE 17.

Changes in the distribution of sodium in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. control - Long Ashton Solution
B. high K - 390 ppm
C. high Mg - 48 ppm

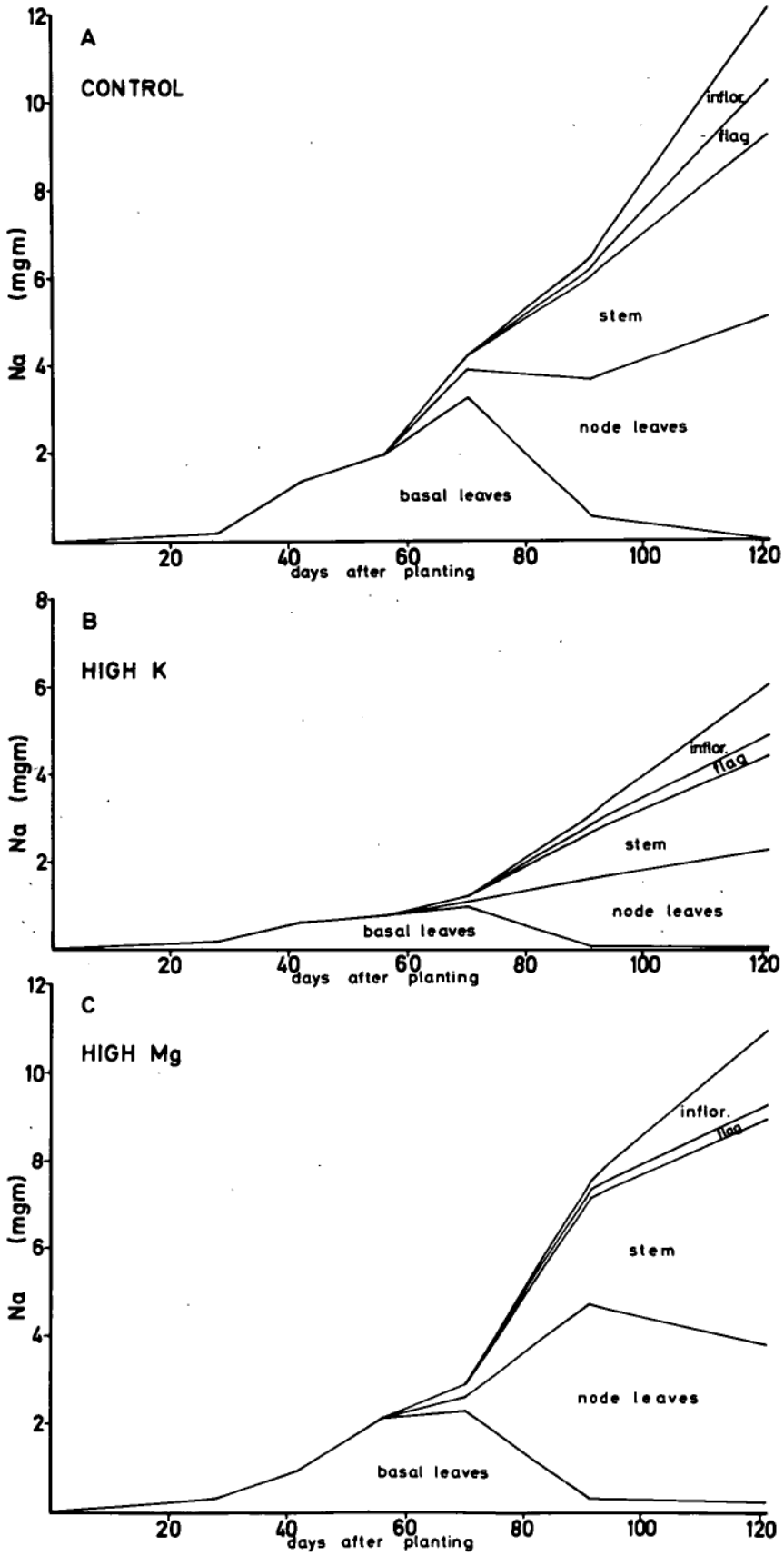

A
CONTROL
inflor.
flag
stem
node leaves
basal leaves
Na (mgm)
days after planting
B
HIGH K
inflor.
flag
stem
node leaves
basal leaves
Na (mgm)
days after planting
C
HIGH Mg
inflor.
flag
stem
node leaves
basal leaves
Na (mgm)
days after planting

FIGURE 18.

Changes in the distribution of phosphorus in the main stem and first tiller of barley plants during the growth period of 121 days, as affected by elevated potassium and magnesium.

A. control - Long Ashton Solution
B. high K - 390 ppm
C. high Mg - 48 ppm

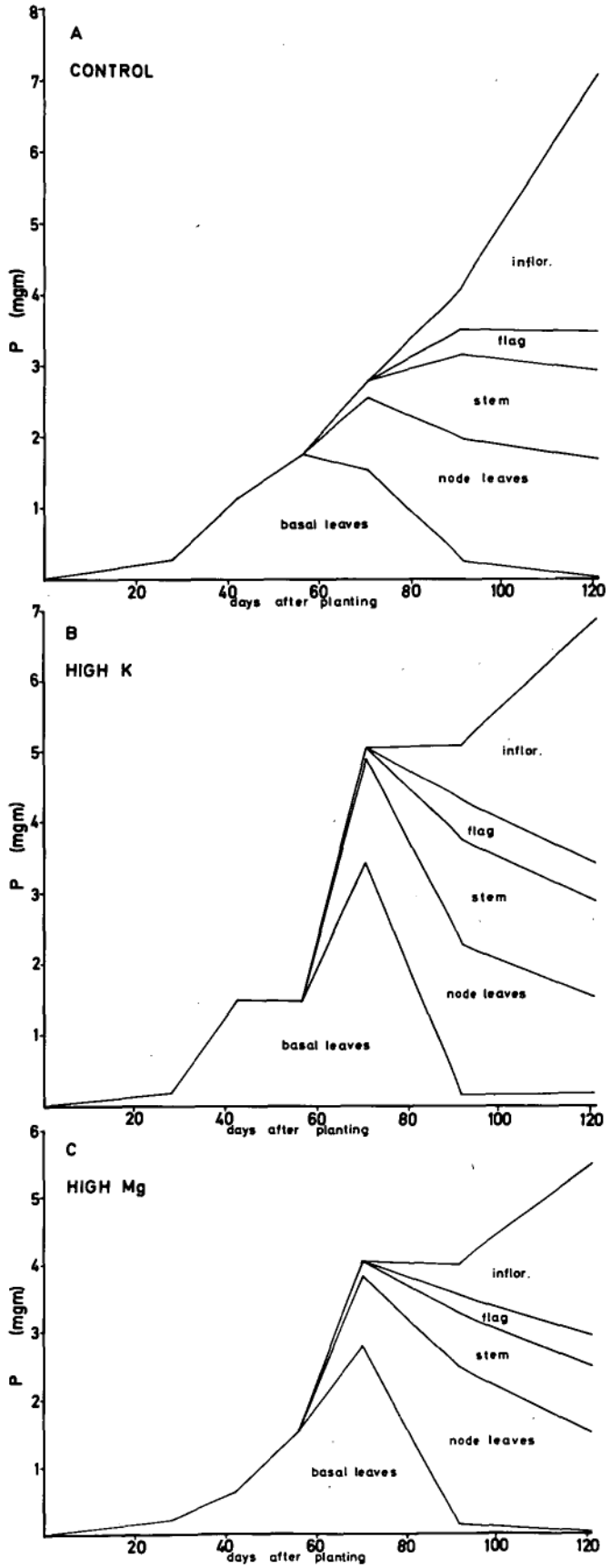

A
CONTROL
P (mgm)
inflor.
flag
stem
node leaves
basal leaves
days after planting
B
HIGH K
P (mgm)
inflor.
flag
stem
node leaves
basal leaves
days after planting
C
HIGH Mg
P (mgm)
inflor.
flag
stem
node leaves
basal leaves
days after planting

TABLE 21

Distribution experiment

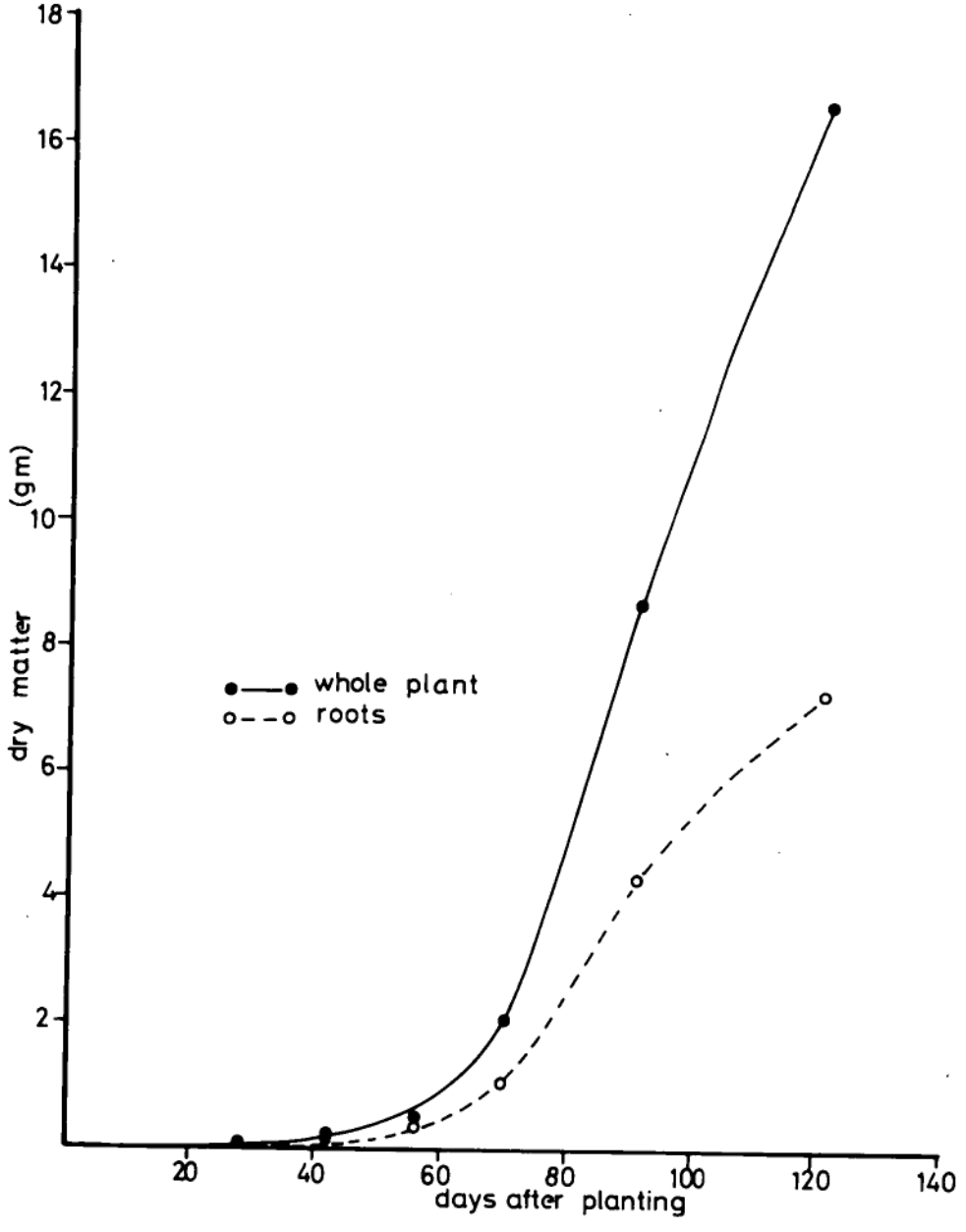
Plant root magnesium content (%)

Harvest (days)	28	42	56	70	91	121
In terms of root dry matter.						
Control	0.265	0.109	0.068	0.068	0.056	0.127
High K	0.147	0.105	0.078	0.076	0.063	0.115
In terms of total plant Mg.						
Control	37.2	21.6	11.4	11.9	15.5	35.0
High K	17.6	13.3	15.4	13.0	19.1	31.8

FIGURE 19.

Development of whole barley plants and their roots (in terms of dry matter) over the 121 day growing period.

Data from high K, normal Mg treatment.


18
16
14
12
10
8
6
4
2
dry matter (gm)
whole plant
roots
20
40
60
80
100
120
140
days after planting

Distribution of phosphorus in the main stem and first tiller (Figure 18), was unaffected by the high potassium level of the medium, except for an accumulation of phosphorous in the basal leaves. High magnesium levels in the medium reduced the total phosphorus content of the main stem and the first tiller.

There was in increase in phosphorus in the basal leaves and a decrease in phosphorus in the inflorescence. This is contrary to the findings of Truog et al.(1947) and Peterson and Berger (1951) who found a greater increase in the phosphorus content of peas following addition of magnesium than after the addition of phosphorus itself. In the present work the total plant phosphorus taken up was also less in the presence of high magnesium (Table 20).

V DISCUSSION

A. Interaction between potassium and magnesium during uptake.

Evidence from whole plant studies in solution culture supports the contention that potassium reduces the uptake of magnesium by plants (Scharrer and Mengel 1960; Komai 1963; Yoshida 1964; Schiedecker 1964; Madhok 1965; Omar and El Kobbia 1965; MacLeod and Carson 1966). Contrary evidence has been advanced by Cain (1953 a & b, 1955) that potassium does not reduce the uptake of magnesium in apples but reduces its translocation from root to tops. The reduction of magnesium in plant tops does not then necessarily reflect a reduction in total plant magnesium.

Data obtained in the present study (Table 15) show that in whole barley plants, potassium reduces the amount of magnesium taken up by the plants, the reduction being apparent quite early in their development. It would appear that, for annuals at least, potassium is capable of restricting magnesium uptake.

This finding suggests that the two ions, potassium and magnesium, may compete at the root surface. The work of Epstein and Hagen (1952) added support to the hypothesis that carriers were involved in ion uptake and that ions could compete for carrier sites in much the same way as enzymes compete for a substrate. Enzyme kinetics applied to the competition between potassium and magnesium in the present study, have clearly shown that competitive inhibition occurs between these two ions. The slope of the magnesium uptake lines on the Lineweaver-Burk plot was increased by the presence of potassium, that is the function K_m/V was increased, without altering the intercept of the lines with the vertical axis (1/v). The maximum velocity of uptake V=62.5 u mol/g/hr was not altered by the presence of the interfering ion so that the Michaelis Constant (K_m) was increased. In this case, the Michaelis constant increased from 2.14 mM in the absence of potassium to 17.2 mM in the presence

of 10 mM KCl and 41.7 mM in the presence of 25 mM KCl. In terms of the carrier hypothesis, this means that potassium and magnesium are in active competition for the same carrier site. This type of competition between a monovalent and a divalent cation has not been reported previously. Earlier reports have been confined to competition between ions of like valence (Steward and Sutcliffe 1959).

Sutcliffe (1957) and Steward and Sutcliffe (1959) have criticised the conclusions of Epstein and Hagen (1952) arguing that when two ions are said to be competing for the same mechanism, absorption of one may be strongly inhibited but that of the other may be unaffected, or even, stimulated. They have claimed that the hypothesis of Epstein and Hagen (1952) requires that when two ions are competing for a site, the uptake of either should be inhibited in the presence of the other. Because of this they question the suitability of the kinetic approach. Study of the uptake of the preferred ion, in the presence of its competitor, would lead to the conclusion that the two ions were not competing for the same site while examination of the absorption of the non-preferred ion could indicate that they were.

This is precisely what has been found in the present study. Examination of the uptake of the non-preferred ion (in this case magnesium) in the presence of the preferred ion (potassium) showed that the two ions were in competition (Figure 4). Examination of the uptake of the preferred ion (in this case potassium) in the presence of magnesium showed that its uptake was stimulated (Figure 5) or unaffected (Figure 6) depending on whether or not there was a common anion present. The common anion associated with stimulation of potassium uptake was chloride. Viets (1944) earlier found that divalent ions, such as calcium and magnesium, stimulated potassium

uptake. Steward and Sutcliffe (1959) pointed out that a common anion, usually chloride, was invariably present when such effects were observed; since large amounts of chloride were taken up, cations must be taken up too, to maintain electrochemical equilibrium. Potassium, which appears much more mobile, is taken up in greater quantities than is magnesium under these conditions. The use of magnesium chloride in the present work thus gave the impression that magnesium had stimulated potassium uptake (Figure 5). When the experiment was repeated using sulphate as the anion of magnesium, no stimulation occurred (Figure 6), suggesting that the stimulatory effect was due to the chloride ion. This explanation is supported by the finding of Epstein, Rains and Elzam (1963) that more cation tended to be taken up when chloride was the anion used while the results of Waisel (1962) can be explained in a similar way.

Failure to demonstrate interference in both directions need not mean that competition does not exist between potassium and magnesium, although Omar and El Kobbia (1965,1966) place this interpretation on their whole plant data. Such experimental findings do not necessarily invalidate the application of the kinetic approach to these studies.

If there is competition between potassium and magnesium for a single site, potassium must inhibit magnesium uptake and vice versa. In the present study, potassium has been shown to interfere with the uptake of magnesium and this may be taken as evidence of competition between the two ions for a carrier site. When potassium uptake was measured to determine if magnesium was in competition with it, no inhibition of potassium uptake was apparent. Nevertheless, it can still be postulated that competition exists for a particular magnesium site as indicated by the initial experiment (Figure 4). Any such inhibition could be masked completely if there were other sites for potassium uptake, for which magnesium

did not compete. Two sites for the uptake of potassium by barley roots have already been postulated by Epstein, Rains and Elzam (1963) who showed that uptake of potassium by one of these sites was subject to little competition from other mono-valent ions, such as sodium. This latter mechanism operated at concentrations below 0.2 mM KCl. Levels of 10 mM and 25 mM KCl were used in the present study, well within the range of the competitive mechanism described by Epstein, Rains and Elzam (1963). It was not possible to explore the effects of potassium levels below 0.2 mM KCl on the uptake of magnesium by detached barley roots in the present work, because the analytical methods available lacked sufficient sensitivity.

It is possible that many sites for the uptake of potassium exist which need not be subject to competition from magnesium. The existence of such sites, in addition to the single specific example already postulated by Epstein, Rains and Elzam (1963), could explain the ineffectiveness of magnesium on the uptake of potassium by barley roots.

Magnesium does not show the competitive ability which might be expected of an ion with an ionic radius of 0.65 Å, particularly as the apparently much more mobile potassium ion has the larger radium of 1.33 Å (Table 22). In addition to greater mobility derived from its smaller size, divalent magnesium should be more able to compete with monovalent potassium for absorption sites if coulombic attraction and adsorption are important steps in the overall mechanism of uptake. However, ion mobility in solution is also a function of the hydrated ion radius, which is considerably larger than the ionic radium in many cases. Some indication of the magnitude of hydrated ion radii is given by the study of hydration energies and hydration numbers, which are estimates of the number of molecules of water associated with an ion in solution (Table 22). It is estimated that potassium has three water molecules associated with each ion, whereas magnesium has 13. As a consequence, magnesium should be much

TABLE 22

Ionic radii, hydration energies and hydration numbers of selected ions

Ion	Ionic radii (Pauling) A°	Hydration energies (Eley & Evans) G°	Hydration numbers (Ulich) N
F^-	1.36	-81	5
Cl^-	1.81	-52	3
Br^-	1.95	-47	2
I^-	2.16	-26	1
Li^+	0.60	-126	5
Na^+	0.95	-107	4
Rb^+	1.48	-75	3
K^+	1.33	-84	3
Mg^+	0.65	-479	13
Ca^+	0.99	-410	10

(Values from Conway and Bockris 1954)

less mobile in solution than potassium. In addition, the large firmly-held sphere of water molecules surrounding the magnesium ion, would hinder its approach to absorption sites as compared with the less heavily hydrated potassium ion. Coulombic attraction between the absorption site and hydrated magnesium ion, being inversely proportional to the square of the hydrated ion radius, would be greatly reduced. These factors, therefore, in addition to the possible existence of numerous potassium uptake sites, could contribute to the greater competitive power of potassium compared to magnesium in ion uptake.

Following on the discovery of ATPase systems for ion uptake in animal cells, it seems likely that ion uptake may also be mediated by ATPase systems in plants (Brown et al. 1965; Gruener and Neuman 1966; Chattopadhyay and Brown 1966; Dodds and Ellis 1966; McClurkin and McClurkin 1967). The mechanism probably involves membrane-fixed ATPase which can engage in vectoral reactions as envisaged by Lehninger (1965). Most ATPases are activated by K^+ and Na^+. However, the ATPase isolated by Gruener and Neuman (1966) from bean roots is Mg^{++}-dependent. Hafkensheid and Bonting (1968) found that urea inactivates the Mg^{++}-dependent ATPase of Escherichia coli without affacting the K^+ and Na^+-dependent enzymes. Urea did not influence magnesium uptake by barley roots in the present work. This aspect requires much more work with the objective of relating ion uptake to the behaviour of the isolated enzyme. In addition isolated ATPases are almost invariably sensitive to the cardiac glycoside, ouabain. Although the enzyme isolated from bean roots by Gruener and Neuman (1966) did not react in this way, both Chattopadhyay and Brown (1966) and Dodds and Ellis (1966) have isolated ouabain-sensitive ATPases from barley roots. However, Mengel (1953) found rubidium uptake by barley roots was insensitive to ouabain.

Such difficulty in relating the behaviour of isolated substances to their behaviour in intact tissues is not a new problem in biochemistry and intensive experimentation with improved techniques may be expected to reconcile these aspects.

Under the conditions of the present study, potassium has reduced the amount of magnesium within the plant and this has been achieved by competition between potassium and magnesium at uptake, which may be interpreted as competition between these two ions for an uptake carrier site utilizable by potassium as well as magnesium, while potassium may be able to enter the plant with equal facility by at least one site not subject to competition by magnesium.

B. Effects of potassium on magnesium status of plants other than direct effects on uptake.

In addition to competition at uptake, it seems that potassium may also effect the magnesium status of plant tissues by mechanisms operative within the plant.

(i) Accumulation in roots: The contention that potassium causes accumulation of magnesium in the roots only and does not reduce the amount of magnesium taken up (Cain 1953 a & b, 1955) is not supported in the present work. Such an effect of potassium could, however, be operative as well as its effect on uptake. The data presented in Figure 7 support this suggestion. In the absence of potassium, the net influx of magnesium into detached roots and into attached roots differed significantly. This difference almost certainly is due to the efflux of magnesium to the plant tops, where these are still available as a sink for magnesium.

When potassium is present two effects are noted. The total net influx of magnesium into whole plants is reduced by competition with potassium at uptake. However, the difference in net influx between detached and attached roots is no longer obvious. This could be explained if potassium inhibited the translocation of magnesium from root to top. The lowest

magnesium level recorded (0.085%) is well above figures quoted for magnesium deficiency in barley (Goodall and Gregory 1947; Wallace 1951) although these authors do not specifically quote data for root magnesium. However, values as low as 0.048% magnesium have been obtained elsewhere in this study in healthy barley roots. It is unlikely, therefore, that the phenomenon under discussion is complicated by the fact that magnesium deficiency levels have been reached.

Analysis of the tops of plants in this experiment, shows that less magnesium reaches them in the presence of potassium, although the amount represents about the same proportion of total plant magnesium as is translocated by plants in the absence of potassium. The results could be explained by the fact that whole plants took up more magnesium in the presence of potassium than did detached roots. When the influx to the tops is added to that to the roots, in the presence of potassium, the total is greater than the influx to detached roots.

An alternative explanation could be that potassium interferes with the translocation of magnesium from the roots. This would be in line with the findings of Cain (1953 a and b; 1955) for apple roots. Some further support is offered by the fact that magnesium accumulates in the roots of maize plants in the presence of high potassium (Table 3). On the other hand, data in Table 15, for Bolivia barley, show that potassium reduced the amount of magnesium in the roots as well as in other parts of the plants. However, in the early harvest at 28 days, there is no change in the amount of magnesium in the roots related to the potassium level. If the values for root magnesium are expressed in terms of total plant magnesium, little effect due to high potassium is seen (Table 21) except early in the growing period and then a slight reduction, not an increase, is shown. It may be that the accumulation of root

magnesium in the presence of potassium occurs only in the early stages of growth, after which the increased rate of root and plant growth (Figure 19) may negate the effect.

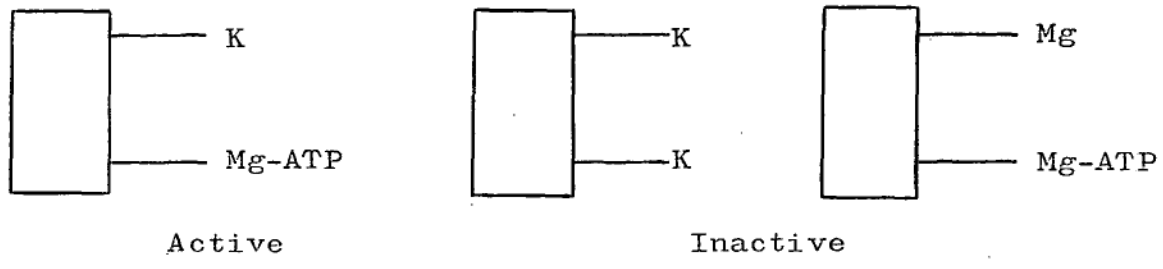
If the accumulation of magnesium in roots is a persistent effect for maize and Proctor barley, as Cain (1953 a and b; 1955) found for apples, the variation in occurrence of the effect could be due to variation in varietal performance. Proctor barley was used in the short term uptake experiment and showed root accumulation of magnesium under the influence of potassium, while Bolivia barley was used in the whole plant sand culture experiments and did not. Although no other data are available relating to the variation in performance of these two varieties, variation in varietal susceptibility to magnesium deficiency has been reported in maize (Foy and Barber 1958) and in celery (Pope and Munger 1953). The mechanism of this variation is unknown. Varietal variation in ability to transport manganese and aluminium from root to top has been described in lucerne (Dessureaux 1958; Ouellette and Dessureaux 1958) and varietal differences in the uptake of potassium by detached tobacco roots have been reported by Hiatt (1963). It is clear, however, that under some circumstances potassium does reduce translocation of magnesium from plant roots.

(ii) Potassium/magnesium ratios: It has been demonstrated that the presence of potassium in the root environment reduces the uptake of magnesium by the plant (Table 15) and thus increases the K/Mg ratio of the plant tissues. Over a number of years the literature has contained many statements to this effect and more recent experiments have yielded confirmation for a number of crops: potatoes (Sluijsmans 1959; Laughlin 1966), rape (Mengel 1960), citrus (Page et al.1963), oats (Jacobsen and Steenbjerg 1964), lucerne (Omar and El Kobbia 1966), tomatoes (Winsor et al.1965) and barley in the present study.

The statement that elevated potassium may reduce magnesium to the level where deficiency symptoms may occur has often been made. Southwick (1943) claimed this for apples and Wallace (1951) for apples and tomatoes. On the other hand, a better prediction of the appearance of symptoms can be made from the K/Mg ratios than from the amount of either element alone (Table 6-8, Figure 12). In this regard the percent potassium content is a particularly bad guide. Walsh and Clarke (1945a) and Ferrari and Sluijsmans (1955) also suggest that K/Mg ratios are more important in the expression of symptoms on potatoes and apples.

With Grosse Lisse tomatoes it would appear that any tissue with a K/Mg ratio above 2.4 is likely to show magnesium deficiency symptoms, while those with a ratio below 1.5 are likely to show potassium deficiency symptoms. Similar proposals have been advanced for other nutrients, particularly iron and manganese: high Fe/Mn ratios in tissues were associated with iron excess or manganese deficiency, low ratios were associated with iron deficiency or manganese excess (Somers and Shive 1942; De kock and Inkson 1962).

The physiological importance of a precise K/Mg ratio in plant tissues is being appreciated more and more as plant functions are discovered which depend on a precise ratio for optimum efficiency. Enzymes which require both Mg^{++} and K^{+} for activation have been found in microorganisms (Priess and Handler 1957, 1958; Ismande 1961; Snoke 1955). These reactions could be important also in higher plants. Hers (1952) pointed out that liver fructokinase reactions require a specific K/Mg ratio for optimum activity. This was said to be due to the fact that the fructokinase enzyme had two reactive sites which could combine with metals or their complexes. An enzyme with Mg-ATP at one site and K at the other may be said to be active and all other combinations inactive:



Active Inactive

Steenbjerg and Jacobsen (1963) suggested that the inhibition of ma gnesium uptake by potassium may be explained on the basis that a similar enzyme is involved. The discovery of ATPases in plant roots (Gruener and Neumann 1966; Chattopadhyay and Brown 1966; Dodds and Ellis 1966) and the postulation of their vectoral action in membranes by Lehninger (1965), increases the likelihood that ATPases mediate in K^+ and Mg^+ transport in a very similar way to that envisaged for fructokinase by Hers (1952).

Differences in behaviour of ATPases from animals, plants and micro-organisms have been found, particularly in relation to sensitivity to ouabain (Mengel 1963; Brown et al. 1965). Hafkenshied and Bonting (1968) suggested that urea inactivated Mg-ATPase in microorganisms. The single experiment carried out in this study on the effect of urea on Mg uptake by detached barley roots (Figures 8 and 9) proved negative. This could have been due to the fact that barley roots ATPase is not sensitive to urea and in this way differs from the ATPase of microorganisms, or to the fact that insufficient urea was used in this experiment.

The findings of Tempest et al. (1966) that a specific K/Mg ratio is required to maintain the stability of micro-organism ribosomes, may also apply to higher plants. Since ribosomes are responsible for the synthesis of plant protein, this is another important reason why specific K/Mg ratios may be required for optimum plant performance. It may explain why high levels of potassium can, in a short time, reduce the dry matter production of plants (Table 13).

(iii) Mobility of plant magnesium: It has been universally accepted that magnesium from older plant leaves could be reallocated to growing points and younger leaves under deficiency conditions (Wallace 1951). Doubts about this statement were expressed by Ruck and Gregory (1955) and Neales (1958). Further doubts were raised by the discovery of Bukovac and Wittwer (1957) that Mg^{28} could not be transferred from the leaves to which it was applied. However, this immobility may be of the type discussed by Millikan and Hanger (1964, 1965) in relation to Ca^{45}, which was considered to be due to adsorption onto the many negatively charged sites within the leaf. When these were saturated with other cations, or non-radioactive calcium in their work, Ca^{45} was found to be mobile.

Oland and Opland (1956) found no evidence that foliar applied magnesium sulphate could be transported to other parts of the plant, but a large body of literature attests to the efficacy of foliar sprays in overcoming magnesium deficiency. In most cases, foliar application is more effective than application via the roots (Boynton et al. 1943; Boynton 1945; Southwick and Smith 1945; Camp 1947; Nicholas 1948; Russell 1954; Fisher and Walker 1945; Walker and Fisher 1957; Winsor et al. 1965; Laughlin 1966). This is in line with the finding in the present study that high levels of magnesium applied to barley roots failed to change the total magnesium level of the plants (Table 15). Chapman and Brown (1943) found the same inability of magnesium applied to the roots to increase the magnesium content of citrus trees. The greater efficacy of foliar applied magnesium in this respect certainly suggests that magnesium applied in this way must be mobile within the plant. Ford (1967) even claimed that foliar applied magnesium could affect the amount of potassium taken up by plant roots.

When tomato plants were transferred to a magnesium free medium in the present study, transport of magnesium from older

to younger leaves took place (Tables 10-11). Transfer of magnesium even took place from older leaves of the plants grown at a low magnesium level, which were already showing signs of magnesium deficiency before the change over. However, the amount of magnesium transferred to the new growth of such plants was much less than the amount transferred from the older leaves of healthy plants. In general the amount of magnesium transferred to the new growth was a function of the magnesium status of the plants, whether this status was achieved by raising the potassium level of the medium or by reducing the level of magnesium.

If the magnesium status of leaves 1-6 (Table 10) are compared, it is found that the leaves of plants transferred to magnesium free conditions contain 41.7 % less magnesium (2.66 mg) than the similar leaves of plants grown in magnesium for the whole period (6.41 mg). In the case of high potassium plants the comparable difference is 40.7 % even though the amount of magnesium in the leaves of the high potassium plants is much lower, 4.25 mg compared with 6.41 mg in similar leaves of the control plants. In the low magnesium treatment the initial amount of magnesium present in leaves 1 - 6 is still lower (2.12 mg), and the reduction consequent on transfer of these plants to magnesium free conditions is 35.8 %. The fact that the same percentage of magnesium in these lower leaves is reallocated from high potassium plants as from the controls, even though the amount originally present was lower, suggests that potassium assists in reallocation. This is in accord with the results of injection of potassium into tomatoes, which will be discussed below.

New growth of high potassium and low magnesium plants, transferred to magnesium free solutions, was showing slight chlorosis at the end of the experiment. The percentage magnesium content of new growth 0.113 % in high potassium plants and 0.131 % in low magnesium plants (Table 11), is below the level quoted for deficient tomatoes by Wallace

(1951). Thus, although reallocation of magnesium took place, it could not keep pace with the demands of newly developing tissues and could not prevent onset of magnesium deficiency symptoms and reduction in the amount of dry matter produced under magnesium free conditions.

Cain(1959) found that chlorophyll was one of the first magnesium compounds to break down under deficiency conditions. Although he knew little of the function of the bulk of leaf magnesium, he took this early breakdown of the chlorophyll molecule to mean that the rest of the leaf magnesium was important to the plant. Neales (1956) found that up to 62% of the magnesium in white clover was present in the fibre and was unextractable with acetone. This magnesium fraction is unlikely to be capable of reallocation under stress of magnesium deficiency. He also found that about 25 % of leaf magnesium was not associated with either the chlorophyll or the fibre of the leaf. It is now known that the majority of this magnesium is associated with the activation of many enzymes (Gaugh and Krauss 1959) and with maintaining the stability of the ATP molecule (Lehninger 1965) and the ribosomes (T'so and Vinograd 1961). Reallocation of this portion of the leaf magnesium would greatly affect the health of the leaf.

As mentioned earlier, it seems possible that high potassium does in fact help with the reallocation of magnesium. Data from leaflets on opposite sides of the leaf above the injected lateral (Table 9) show that added potassium reached only one side of that leaf. This coincided with the symptom distribution (Figure 11). The affected side had less magnesium than the unaffected side, suggesting that the high potassium level may have remobilized the leaf magnesium and aided its transport from the leaf. In the examination of distribution of magnesium as influenced by variation in potassium and magnesium levels in the medium (Figure 15, a, b and c) the nodal leaves and to a lesser extent the stem

and flag, contain less magnesium than they do in the control plants. This fact would also be consistent with increased reallocation of magnesium under the influence of high potassium although it could simply be that less magnesium is taken up by these parts when high potassium levels prevail.

(iv) Distribution of nutrient ions during plant development: Potassium and Magnesium: High potassium (Table 13) reduced the dry matter production of barley roots. The dry matter production of the main stem and first tiller was not affected, the main reduction being in root weight and in tiller production. The number of tillers was reduced in the high potassium treatment (Table 17). This was possibly due to the reduction of magnesium levels. Magnesium is actively associated with growth processes and initiation of new growing points is likely to be reduced by anything which depresses magnesium level.

High magnesium levels in the medium depressed the amount of potassium taken up by barley plants. This cannot be explained in terms of competition at uptake because magnesium was demonstrated earlier to be an ineffective competitor against potassium at this level. The antagonism may therefore be associated with other facets of plant metabolism. The mechanism of this behaviour is all the more difficult to explain because the high magnesium level in the medium did not cause any increase in the amount of plant magnesium. Chapman and Brown (1943) made a similar observation for citrus. Contrary to these findings, Omar and El Kobbia (1965) failed to find any depression of plant potassium by elevated levels of magnesium in the medium.

One of the interesting features of the uptake of potassium by the main stem and first tiller was that their potassium content reached a maximum at 91 days after sowing in both high potassium and high magnesium treatments (Figure 14b).

The increased amount of potassium which the inflorescence contained as it developed therefore came from other plant parts; in particular the stems and node leaves. Table 16 shows that the percent potassium in the infloresence did not change with treatment but remained at the same level in both high potassium and control treatments. This is in keeping with the apparent mobility of potassium in the plant. The needs of the developing inflorescence can be supplied from other parts of the plant. Barber and Humbert (1963) reported that a potassium deficient plant and one with three times as much potassium, both contained about the same amount of potassium in the new growth.

There was no reduction in the magnesium contained in the leaves as the inflorescence developed and increased its magnesium demand. The required magnesium must have come from continued uptake or from the other parts of the plants. Reductions in magnesium levels of some tillers (Table 17) may suggest that at least some magnesium required for inflorescence development was gained at the expense of these plant parts. Cain (1955) with apples and Fudge (1939) with citrus, suggested that reallocation of magnesium from spur leaves to developing fruit caused reduction of magnesium levels in these leaves, often to the level of deficiency. In the present study, there was no evidence that reallocation of flag magnesium took place to the developing inflorescence (Figure 15 b). However, the magnesium content of the node leaves and flag decreased higher up the stem. At the extremes the leaf at the first node had a magnesium content of 0.568 % compared with 0.253 % for the flag. This suggests at least some preferential movement of Mg to the inflorescence at the expense of the flag and that under deficiency conditions, some reallocation of flag magnesium to the inflorescence may occur. Fudge (1938) placed great emphasis on the demand of the

developing seed for magnesium in relation to development of magnesium deficiency. He distinguished between resistant and susceptible varieties of grapefruit on the basis of their seedy or seedless character.

Even in barley plants grown in a medium containing adequate amounts of magnesium for normal plant growth, the presence of high levels of potassium resulted in a reduction of the magnesium content of some tillers below 0.2 % the critical level for the onset of hypomagnesaemia in grazing stock (Todd 1961; Russell and Duncan 1956; Rook and Storry 1962; Cairney et al. 1964).

The data for the whole plant (Table 13) show that both high potassium and high magnesium reduced the dry matter production of plants. Fuziwara and Iida (1962) found high magnesium caused excessive magnesium uptake and reduced the yield of rice. In the present study with barley, however, this reduction in dry matter production is achieved without the high magnesium levels causing any rise in plant magnesium content (Table 15). The data also show that high magnesium reduces the total amount of potassium taken up by barley plants (Table 15). Van Itallie (1938) with ryegrass, Chapman and Brown (1943) with citrus, and Kloke (1964) with oats and rape have obtained similar results. However, the short term uptake studies with detached roots have shown that competition will not explain the phenomenon. Omar and El Kobbia (1966) showed no effect of magnesium on the potassium uptake of lucerne. The effect obtained here must be due to the depression of plant yield and is not associated with any depression in the percent magnesium in the plants.

The data presented (Table 13) show that elevation of either potassium or magnesium levels in the nutrient solution has a dramatic and rapid effect on the dry matter yield of the plants.

The physiological importance of a precise K/Mg ratio within the plant has already been discussed, particularly in relation to the stability of ribosomes. As it is the function of the ribosomes to decode messenger RNA and carry out protein synthesis (Bonner J. 1965), any disturbance of the K/Mg ratio will quickly be reflected in depressed plant yield.

Calcium and Sodium: In this study, high potassium and magnesium both reduced plant calcium content. Fuziwara and Iida (1962) found that potassium raised leaf calcium, but this was in the presence of low magnesium. However, the present findings agree with those of Scharrer and Mengel (1960) who found that high potassium reduced both calcium and magnesium levels in the leaves and stalks of several plant species.

The sodium levels of all plant fractions were greatly reduced in the main stem and first tiller in the presence of high K (Figure 17) and the same dramatic reduction was shown in values for the whole plant (Table 19). Such large changes have led some authors to emphasise the role of all cations. Van Itallie (1938) showed that Mg + Ca + K + Na = 200 me/100 g dry matter in Italian ryegrass, even though values for individual elements varied widely. Alloway and Pierre (139), Stanford et al. (1942) and Lucas and Scarseth (1947) emphasised the $\frac{Ca + Mg}{K}$ balance.

Little is achieved, however, by such arithmetical calculations unless they can be usefully related to plant mechanisms. Gauch and Krauss (1959) stress the importance of the Ca/Mg ratio in certain enzyme reactions, membrane permeability and hydration of cell colloid. The importance of sodium is perhaps also related to its function, along with potassium and magnesium, in the activation of ATPases, apparently associated with ion uptake by plant cells (Gruener and Neumann 1966; Chattopadhayay and Brown 1966; McClurkin and McClurkin 1967). It is difficult to reconcile the apparent specific

function of sodium in this regard with the lack of direct evidence to show that it is essential for any great number of plant species.

Phosphorus: Early workers (Jacob 1955) placed much stress on correlations between phosphorus and magnesium in plant tissues. It has even been suggested that magnesium is a carrier for phosphorus (Truog et al. 1947). Magnesium has been found to activate many enzyme reactions involving phosphate and this accounts for the concentration of both these ions in actively developing plant tissues (Bear et al. 1951). Magnesium also structurally stabilises the ATP molecule (Lehninger 1965).

Stenlid (1959) suggested that magnesium stimulated the uptake as well as transport of phosphorus. In the present work both the total plant phosphorus (Table 20) and the inflorescence phosphorus (Figure 18) were reduced by high levels of magnesium in the medium. This latter observation is in contrast to the work of Peterson and Berger (1951) who found that magnesium increased the phosphorus content of pea seeds.

It seems likely that the often cited correlation between phosphorus and magnesium in plant tissues is associated with their related functions in plant metabolism.

C. Conclusions.

Elevated levels of potassium had a depressing effect on the uptake of magnesium by plants and on their dry matter production. This antagonism may be explained in the following ways:

(1) Potassium inhibits the uptake of magnesium by plants and competition for a single carrier site has been demonstrated by methods based on Michaelis-Menten enzyme kinetics. Competition was not exhibited in the reverse sense, possibly due to the fact that there may be more than one site for potassium uptake, and that these include sites which are not subject to competition from magnesium. In addition, it is suggested that

the larger hydrated radius of the magnesium ion may reduce its ability to compete effectively with the smaller hydrated potassium ion.

(2) Accumulation of magnesium may occur in the roots of plants in the presence of high levels of potassium.

(3) under magnesium deficient conditions a proportion of leaf magnesium may be reallocated from the older leaves to new leaves and growing points.

(4) High levels of leaf potassium may assist in the movement of magnesium out of leaves.

The apparent stimulation of potassium uptake by detached barley roots in the presence of a divalent cation (the so-called "Viets effect") has been shown to be due to the presence of a common anion, in this case chloride.

High potassium levels in the medium have also been shown to reduce the uptake of cations other than magnesium, notably sodium. Potassium had little effect on the uptake of phosphate and high levels of magnesium reduced its uptake.

The depressing effect of high potassium and high magnesium on the dry matter yield of plants has been related to the importance of the K/Mg ratio in plant tissues. This has been shown to be a better indication of symptom expression than the level of either ion alone. It is suggested that depression in yield of dry matter is linked with the importance of this ratio in maintaining ribosomal stability and protein synthesis.

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APPENDIX A.

1. Potassium-magnesium antagonism at uptake

(a) The effect of potassium ion on the uptake of magnesium

Data upon which Figures 3 and 4 are based

Treatment	$\frac{1}{S}$	Uptake % Mg				V	$\frac{1}{V}$
		I	II	III	Mean	μ mol/g/hr	
0 mM KCl^+							
2.5 mM $MgCl_2$	0.400	0.141	0.140	0.172	0.151	31.9	0.031
4.0 "	0.250	0.185	0.184	0.190	0.186	38.2	0.026
7.5 "	0.133	0.208	0.207	0.213	0.209	43.0	0.023
15.0 "	0.067	0.268	0.240	0.246	0.251	51.6	0.019
25 mM KCl^+							
2.5 mM $MgCl_2$	0.400	0.015	0.015	0.018	0.016	3.3	0.304
4.0 "	0.250	0.028	0.022	0.022	0.024	4.9	0.203
7.5 "	0.133	0.060	0.054	0.054	0.056	9.5	0.106
15.0 "	0.067	0.083	0.077	0.083	0.081	16.7	0.060

Data upon which Figures 3 and 4 are based continued

Treatment	$\frac{1}{S}$	Uptake % Mg				V μ mol/g/hr	$\frac{1}{V}$
		I	II	III	Mean		
0 mM KCl+							
2.5 mM $MgCl_2$	0.400	0.141	0.128	0.146	0.138	28.4	0.035
4.0 "	0.250	0.185	0.187	0.173	0.182	37.4	0.027
7.5 "	0.133	0.208	0.210	0.203	0.207	42.6	0.023
15.0 "	0.067	0.268	0.298	0.246	0.271	55.7	0.018
10 mM KCl+							
2.5 mM $MgCl_2$	0.400	0.039	0.038	0.038	0.038	7.8	0.128
4.0 "	0.250	0.057	0.054	0.052	0.054	11.1	0.090
7.5 "	0.133	0.083	0.080	0.078	0.081	16.7	0.060
15.0 "	0.067	0.114	0.118	0.109	0.114	23.4	0.043

(b) The effect of magnesium ion on the uptake of potassium

Data upon which Figure 5 is based

Treatments	$\frac{1}{S}$	Uptake % K				V μ mol/g/hr	$\frac{1}{V}$
		I	II	III	Mean		
0 mM $MgCl_2$ +							
5.0 mM KCl	0.200	0.71	0.50	0.59	0.60	7.8	0.130
7.5 "	0.133	0.76	0.79	0.74	0.76	9.7	0.103
10.0 "	0.100	0.96	0.89	0.79	0.88	11.3	0.089
25.0 "	0.040	1.32	0.99	1.25	1.19	15.2	0.068
25.0 mM $MgCl_2$ +							
5.0 mM KCl	0.200	0.91	0.81	0.65	0.79	10.1	0.099
7.5 "	0.133	0.96	0.86	0.90	0.91	11.6	0.086
10.0 "	0.100	0.96	1.01	1.05	1.01	12.9	0.077
25.0 "	0.040	1.32	1.31	1.30	1.31	16.8	0.060

(b) The effect of magnesium ion on the uptake of potassium

Numerical data for repeat experiment

Treatments	$\frac{1}{S}$	Uptake % K				V μmol/g/hr	$\frac{1}{V}$
		I	II	III	Mean		
0.0 mM $MgCl_2$ +							
5.0 mM KCl	0.200	1.71	1.20	1.59	1.50	9.6	0.104
7.5 "	0.133	1.51	1.90	1.59	1.67	10.7	0.094
10.0 "	0.100	1.41	1.90	1.61	1.64	10.5	0.095
25.0 "	0.040	1.51	2.10	2.30	1.97	12.6	0.079
25.0 mM $MgCl_2$ +							
5.0 mM KCl	0.200	1.72	2.32	2.17	2.07	13.2	0.075
7.5 "	0.133	2.42	2.53	2.07	2.33	14.9	0.067
10.0 "	0.100	2.53	2.32	2.17	2.34	15.0	0.067
25.0 "	0.040	2.85	2.85	2.45	2.72	17.4	0.057

(c) The effect of magnesium on potassium uptake when salts of different anions are present

Data upon which Figure 6 is based

Treatments	$\frac{1}{S}$	Uptake % K				V μ mol/g/hr	$\frac{1}{V}$
		I	II	III	Mean		
0 mM $MgSO_4$ +							
5.0 mM KCl	0.200	0.91	0.80	0.81	0.84	10.7	0.93
7.5 "	0.133	1.01	1.05	0.86	0.97	12.4	0.81
10.0 "	0.100	1.06	1.10	1.06	1.07	13.7	0.73
25.0 "	0.040	1.42	1.41	1.37	1.40	18.0	0.56
25 mM $MgSO_4$ +							
5.0 mM KCl	0.200	0.84	0.80	0.74	0.79	10.1	0.99
7.5 "	0.133	1.04	1.00	1.04	1.03	13.2	0.76
10.0 "	0.100	1.14	1.05	1.09	1.09	13.9	0.72
25.0 "	0.040	1.25	1.16	1.15	1.19	15.2	0.66

(d) Uptake of magnesium by barley seedlings in the presence and absence of potassium, compared with uptake by detached roots

Data for uptake by seedlings graphed in Figure 7

Roots

Treatments	Uptake Mg %				V
	I	II	III	Mean	μ mol/g/hr
0.0 mM KCl +					
2.5 mM $MgCl_2$	0.126	0.126	0.141	0.131	26.9
4.0 "	0.170	0.152	0.141	0.154	31.7
7.5 "	0.170	0.168	0.168	0.169	34.7
15.0 "	0.193	0.185	0.241	0.206	42.4
25 mM KCl +					
2.5 mM $MgCl_2$	0.015	0.018	0.020	0.018	3.7
4.0 "	0.035	0.037	0.057	0.043	8.8
7.5 "	0.052	0.055	0.067	0.058	11.9
15.0 "	0.075	0.065	0.093	0.078	16.0

Data for uptake by seedlings graphed in Figure 7 continued

Tops

Treatments	Uptake Mg %				V
	I	II	III	Mean	μ mol/g/hr
0.0 mM KCl +					
2.5 mM $MgCl_2$	0.068	0.079	0.088	0.078	16.0
4.0 "	0.096	0.093	0.083	0.091	18.7
7.5 "	0.104	0.094	0.105	0.101	20.8
15.0 "	0.121	0.110	0.146	0.126	25.9
25 mM KCl +					
2.5 mM $MgCl_2$	0.011	0.010	0.011	0.011	2.3
4.0 "	0.016	0.020	0.034	0.023	4.7
7.5 "	0.036	0.061	0.039	0.045	9.2
15.0 "	0.050	0.042	0.057	0.050	10.3

(e) Effect of urea on magnesium uptake by detached barley roots

Data upon which Figures 8 and 9 are based

Treatments	$\frac{1}{S}$	Uptake Mg %				V μ mol/g/hr	$\frac{1}{V}$
		I	II	III	Mean		
0.0 M urea +							
2.5 mM $MgCl_2$	0.400	0.118	0.108	0.118	0.115	23.6	0.042
4.0 "	0.250	0.121	0.111	0.121	0.118	24.3	0.041
7.5 "	0.133	0.133	0.138	0.148	0.139	28.6	0.035
15.0 "	0.067	0.148	0.148	0.148	0.148	30.4	0.033
0.2 M urea +							
2.5 mM $MgCl_2$	0.400	0.118	0.110	0.118	0.115	23.6	0.042
4.0 "	0.250	0.121	0.125	0.118	0.121	24.9	0.040
7.5 "	0.133	0.148	0.150	0.133	0.143	29.4	0.034
15.0 "	0.067	0.158	0.150	0.148	0.152	31.3	0.032

APPENDIX B.

2. Potassium and magnesium uptake in the absence of competition at uptake

(a) The effect of applying potassium and magnesium to separate parts of a split root system

Replicate data from split root experiment (Table 3)

Treatment	Plant Part	Dry Wt. (g)			Mg %			K %		
		I	II	Mean	I	II	Mean	I	II	Mean
1/1	Top	0.190	0.196	0.193	0.598	0.748	0.673	2.56	2.98	2.77
	Root L.	0.038	0.046	0.042	0.233	0.273	0.253	6.02	5.40	5.71
	" R.	0.088	0.094	0.091	0.393	0.295	0.344	4.51	3.81	4.16
2/2	Top	0.201	0.231	0.216	0.251	0.317	0.284	2.59	1.77	2.18
	Root L.	0.111	0.141	0.126	0.218	0.172	0.195	6.01	6.87	6.44
	" R.	0.070	0.080	0.075	0.067	0.101	0.084	4.11	3.59	3.85
3/4	Top	0.147	0.165	0.156	0.266	0.328	0.297	1.98	1.10	1.54
	Root L.	0.085	0.075	0.080	0.101	0.077	0.089	2.47	3.27	2.87
	" R.	0.236	0.266	0.251	0.256	0.226	0.241	2.02	2.52	2.27
3/5	Top	0.201	0.185	0.193	0.600	0.636	0.618	1.46	2.18	1.82
	Root L.	0.071	0.055	0.063	0.217	0.193	0.205	2.04	2.64	2.34
	" R.	0.096	0.118	0.107	0.630	0.702	0.666	4.63	4.13	4.38

APPENDIX C.

Data on which Table 9 is based

Treatment	Proximal Side (2)		Distal Side (3)
	K (mg)	Mg (mg)	Mg (mg)
Control	1.84	0.413	0.390
Normal K, infected K	2.52	0.355	0.378
High K, infected K	3.44	0.372	0.389
L S D 1%	0.036	0.032	N.S.

(2) Harvested from site 2, Figure 11.

(3) " " site 3, " 11.